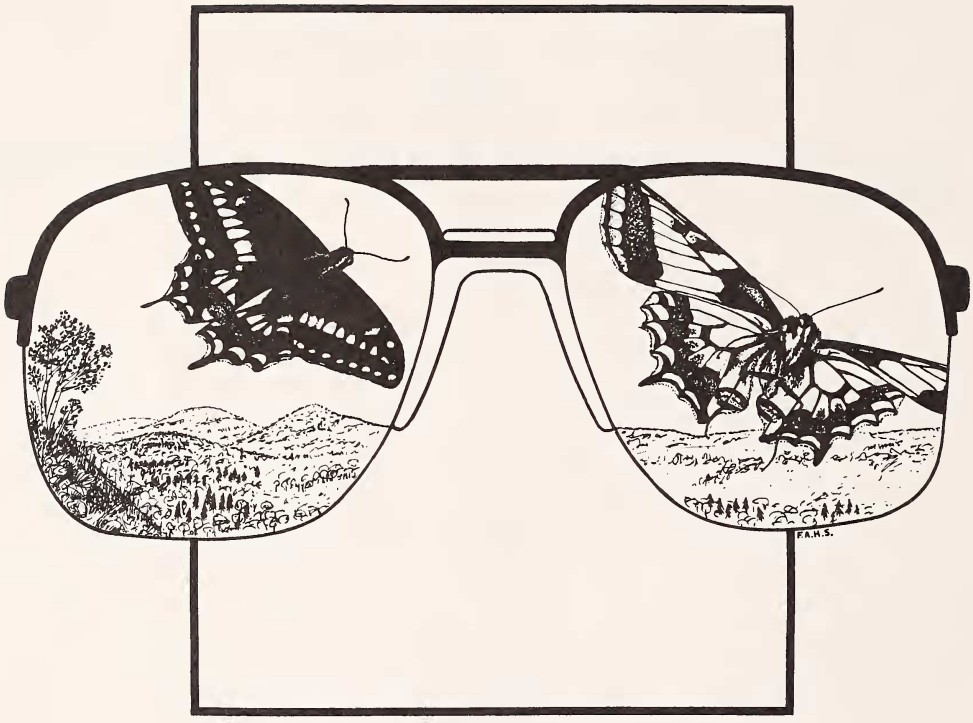
F.A.H.S.

EVOLUTION OF THE *PAPILIO MACHAON* SPECIES GROUP IN WESTERN CANADA (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT

Three species of the Papilio machaon group live in western Canada: P. machaon, P. zelicaon *and* P. polyxenes. *Most specimens of these three species are distinguished on the basis of morphological, electrophoretic or ecological characters. However, all three species hybridize along zones of parapatry, as well as in restricted areas within regions of sympatry.*

All populations of the species group whose larvae eat Artemisia dracunculus *are considered subspecies of* P. machaon. *Also* P. machaon pikei *(type locality: Dunvegan, Alberta) is described as a new subspecies from the Peace River region of northern Alberta and British Columbia.* P. m. avinoffi *and* P. kahli *are considered different expressions of hybridization between* P. machaon *and P. polyxenes, while* P. nitra *is treated as a genetically integrated morph within* P. zelicaon.

Three separate principal components analyses (PCAs), on 10 electrophoretic loci, 11 wing and body color characters, and the combined data set, respectively, gave very similar relative distributions of individuals and populations. Hybrid populations had intermediate mean character values, but much broader ranges of variation than those of the parental species. Enzyme genotypes were tested for conformance to Hardy-Weinberg proportions, with the same loci showing major interruptions in gene flow in some regions, but not in areas where hybrid swarms had formed. Discriminant function analyses of specimens reared on different foodplants supported the conclusions based on PCAs, and gave better species separations in some regions.

The P. machaon *group includes a wide variety of populations associated with different foodplant, habitat and climate conditions. The genetic versatility of the group leads either to ecological divergence between populations, or to localized genetic merging. Large interspecific hybrid populations have formed in central and southern Alberta (*P. zelicaon X machaon*) and in central Manitoba (*P. polyxenes X machaon*), and show varying amounts of ecological isolation from the parental species. On the other hand,* P. m. pikei *is a grassland race which was probably derived early in the Holocene from arctic/alpine populations of* P. machaon. *Hybrid swarm formation predated habitat alteration by European settlers in central Alberta, but may have been a more recent and agriculturally related phenomenon in central Manitoba. Both* P. zelicaon *and* P. machaon *also show introgression of a black wing morph from* P. polyxenes. *This morph has moved far beyond the range of* P. polyxenes, *and such specimens show electrophoretic and ecological characteristics identical to those of the populations of* P. zelicaon *and* P. machaon *in which they are now found.*

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In general, allopatric differentiation and peripheral race formation appear to account for most of the systematic structure of the P. machaon *group, though gene exchange between species is also an important factor. The presence of a widespread but uneven pattern of gene flow among the species of the* P. machaon *group necessitates a loose application of current species concepts, and causes considerable uncertainty in phylogenetic reconstructions.*

Comparison of features of the P. machaon *species group with those of potential sister groups in the genus* Papilio *indicates that color pattern of the ancestral stock of the former was probably like that of* P. machaon *itself, and that the larvae were probably umbellifer-feeders. The* P. machaon *group contains* P. alexanor, *which has problematical, though basal, affinities to the remaining four lineages (1,* P. machaon + hospiton*; 2,* P. zelicaon*; 3,* P. polyxenes + joanae + brevicauda*; and 4,* P. indra*). The Holarctic* P. machaon *lineage is older than the other three, which are Nearctic in distribution. Relationships of the latter three lineages to one another are unclear, and their divergence is represented as a trichotomy. Calculation of Nei's genetic distance suggests that* P. machaon, P. zelicaon *and* P. polyxenes *arose in Pliocene time.*

North America was invaded via *Beringia by the ancestral stock of the* P. machaon *group and, during Pleistocene time, by* P. machaon *itself. Environmental changes, particularly glaciation, caused several periods of range expansion and retraction. Differentiation in isolation led to shifts in ecological features, such as larval foodplants, as well as morphological features and electromorph frequencies. Subsequent contact led to genetic introgression and hybridization, depending in part on the extent to which isolates had diverged ecologically. These events are reflected in western Canada in the genetic structure and relationships of: three species; five subspecies of* P. machaon*; two combinations of hybrid swarms; and evidence of introgression, particularly of genes for black wing morphs.*

RÉSUMÉ

Trois espèces du groupe Papilio machaon *sont retrouvées dans l'Ouest Canadien:* P. machaon, P. zelicaon *and* P. polyxenes. *La plus part des spécimens de ces trois espèces se distinguent sur la base de charactères morphologiques, électrophorétiques et écologiques. Toutefois, des individus hybrides de ces trois espèces sont retrouvés aux abords des zones parapatriques, ainsi que dans des endroits restreints à l'intérieur des régions sympatriques.*

Toutes les populations de l'espèce groupe Artemisia dracunculus *dont les larves se nourissent, sont considérées comme sous-espèces de* P. machaon. *Une nouvelle espèce,* P. machaon pikei *(localité type: Dunvegan, Alberta) est décrite pour la région de Peace River, au nord de l'Alberta et de la Colombie-Britanique.* P. m. avinoffi *et* P. kahli *sont considérés comme différentes expressions de l'hybridation de* P. machaon *et* P. polyxenes, *tandis que* P. nitra *est considéré comme un morphotype génétiquement intégré à* P. zelicaon.

Trois différentes Analyses en Composantes Principales (ACPs) effectuées respectivement sur 10 loci électrophorétiques, 11 caractères basés sur la couleur des ailes et du corps, et sur un groupe combiné de ces caractères, ont produit des distributions relatives très similaires pour les populations et les individus. Les populations hybrides démontrent des caractères moyens de valeurs intermédiaires, mais possèdent des variations bien supérieures à celle des espèces parentales.

Les enzymes génotypiques son testés pour conformité aux proportions de Hardy-Weiberg, utilisant les même loci demontrant une interruption majeure du courant d échange génétique de quelques régions, mais non dans les régions où les essaims hybrides se sont formés. Une analyse en fonctions discriminantes utilisant les spécimens écimens élevés sur différentes source de nouriture, supportent les conclusions basées sur les A.C.P., et demontre pour quelques regions une meilleure séparation des espèces.

Le groupe P. machaon *inclut une grande variété de populations associées à différentes sources alimentaires végétales, habitats et conditions climatiques. La versatilité génétique du groupe conduit soit à une divergeance écologique, soit à des combinaisons génétiques localisées. De larges populations hybrides se sont formées dans le centre et le sud de l'Alberta (*P. zelicaon X machaon*) et dans le Maitoba central (*P. polyxenes X machaon*). Ces populations démontrent différents degrés d'isolation écologique de leurs espèces parentales. Toutefois,* P.m. pikei *considéré comme une espèce des prairies, a probablement évoluè au début de l'Holocène, d'une population arctique/alpine de* P. machaon. *La formation d'essaims hybrides dans l'Alberta centrale, précède la période d'altération de l'habitat induite par l'établissement des*

colons Européens; mais est probablement plus récente et reliée à l'agriculture dans le Manitoba central. P. zelicaon *ainsi que* P. machaon *démontrent l'intégration d'un morphotype à aile noire provenant de l'espèce* P. polyxenes. *Ce type s'est réparti bien au delà de l'aire de distribution de* P. polyxenes, *et de tels spécimens démontrent des charactères électrophorétiques et écologiques identiques à ceux des populations de* P. zelicaon *et* P. machaon *dans lesquelles ils sont maintenant retrouvés.*

De façon générale, la différenciation allopatrique et la formation de races périfériques semblent être responsable d'une grande portion de la structure phylogénétique du groupe P. machaon, *bien que l'échange génétique interspécifique soit aussi un facteur important. La présence d'un courant d'échanges génétiques largement répendu, mais irrégulié, entre les espèces du groupe* P. machaon *nécessite une utilisation au sens large du concept d'espèces, et de ce fait induit de considérables incertitudes lors de la reconstitution phylogénétique.*

La comparaison des traits caractéristiques du groupe-espèce P. machaon *à ceux de potentiels groupes-soeurs dans le genre* Papilio, *indique le patron de couleurs de la souche ancestrale était probablement comme celui de* P. machaon *lui-même, et que les larves se nourissaient probablement de plantes umbellifères. L'espèce* P. alexanor, *qui fait parti du groupe* P. machaon, *a des rapports fondamentaux mais problématiques aux quatres autres lignées (1,* P. machaon + hospiton; *2,* P. zelicaon; *3,* P. polyxenes + joanae + brevicauda; *and 4,* P. indra*). Parmi les quatres lignées, la lignée Holarctique* P. machaon *est plus ancienne que les trois autres qui sont de distribution Nearctique. Les rapports entre les trois lignées néarctiques sont ambigus et ainsi la divergence est décrite en trichotomie. Le calcul de distance de Nei semble indiquer que* P. machaon, P. zelicaon *et* P. polyxenes *proviennent de l'âge Pliocène.*

L'amérique du nord a été envahie via le Beringia par la souche ancestrale du groupe P. machaon *et durant l'âge Pleistocène par* P. machaon *lui-même. Des changements d'environnement en particulier la glaciation, ont causé plusieurs periodes d'expansion et de rétraction de distribution. Les différences d'isolement ont mené aux changements de caractères écologiques tels que plantes-hôtes des larves autant que caractères morphologiques et fréquences d'electomorphs. Le contact subséquent a menê à l'introgression et à l'hybridisation, selon le degré de divergence écologique des isolées. Ces évennements se sont réflechis dans l'ouest du Canada par la structure génétique et les rapports entre trois espèces; cinq sous-espèces de* P. machaon, *deux combinaisons de deux essaims hybrides; et l'évidence d'introgression, en particulier les gènes pour les morphs aux ailes noires.*

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INTRODUCTION

The genus *Papilio* traditionally includes 30 to 40 species groups, of which the *Papilio machaon* L. group is one. Adults of the group are predominantly black and yellow (Plates 1–3), and are relatively large (forewing length: 3.5 to 5.0 cm). The *P. machaon* group is principally defined by larval characters, especially a color pattern of black segmental bands and by use of hostplants in the families Umbelliferae or Compositae.

Opinions about the number of species included within the *P. machaon* group range from four (Eller, 1939) to between 10 and 20 species (*e.g.,* Remington, 1968a). Eight species are

recognized in this study, and three of them are dealt with in detail. There is much less difference of opinion about the limits of the group itself, with most recent authors following Monroe (1961).

Most of the uncertainty about the number of species which should be recognized within the *P. machaon* group is caused by discordant character variation. For example, *P. machaon* and *P. hospiton* Géné remain distinct and easy to distinguish where they contact each other on Corsica and Sardinia, but *P. machaon* has races in North Africa and the Arabian peninsula which are much more similar to *P. hospiton* (Clarke and Larsen, 1986). Wing and body color pattern, and wing shape, have been the main morphometric characters used to distinguish among *P. machaon* group species. However, for identifications of *P. machaon*, *P. zelicaon* Lucas and *P. polyxenes* Fabricius, no one character is completely dependable. Most diagnoses list several characters, and there has been no effort published previously to quantify rigorously these differences using multivariate techniques. The presence of several color polymorphisms within populations has also been a consistent source of taxonomic confusion. The most notable example is the adult morph with black wings, whose features are probably determined by homologous alleles in different species.

Other kinds of taxonomic characters have shown only limited utility. Differences in male genitalia, which are taxonomically valuable in many groups in the Papilionidae, are of minor importance in the *P. machaon* group. In North America adults of only one species, *Papilio indra* Reakirt, can be consistently distinguished on this basis. Use of chromosomal characters (Maeki and Remington, 1960; Maeki, 1976; Clarke *et al.*, 1977) involves substantial technical difficulties. Although gel electrophoresis has been useful for elucidating systematic relationships in many taxa, there have been no reports about variation of enzyme alleles in the *P. machaon* group.

The *P. machaon* species group has a holarctic distribution. It occurs throughout North America and in higher elevations as far south as Peru and Venezuela. It also ranges across Eurasia, southward to South China and North Africa. The group is represented in virtually any vegetation zone in this region. Different ecological races occupy habitats as varied as arctic tundra, high altitude steppe, Saharan desert oases, temperate coastal forest, vegetable gardens and citrus orchards. However, the western United States and Canada is the only part of the range of the *P. machaon* group with extensive sympatry between species. All other regions support only a single species, or a contact zone between two species which is maintained in part by habitat segregation.

Studies of populations of the *P. machaon* group in sympatry are few, based principally on samples from geographically distant localities. Comparisons among many samples show either marked phenetic or ecological differences or a confusing interplay of character variation. Clearly, intensive surveys are needed of population variation in regions of sympatry or parapatry between major species of the *P. machaon* group. As well, there has been little explicit recognition of natural hybridization among species in the group. Since there is evidence of hybridization among the three species included in this study, and virtually all studies on hybrid zones in other taxa involve only two species, work on the *P. machaon* group is of significance to the general study of hybrid phenomena.

Historical Perspective

The historical context of work on the *machaon* group has influenced many of the resulting taxonomic decisions. In particular, the pattern of exploration of new regions and changing

motivations for research have left a diverse legacy of names for taxa. These names represent a number of major stages in the development of systematics as a separate discipline.

The recognized starting point for modern taxonomy, Linnaeus' *Systema Naturae*, Tenth Edition (1758), contained the description of *P. machaon* itself, the type species for the genus *Papilio* and, by extension to the Papilioniodea, it is the type species for all butterflies. New names such as *P. polyxenes* (Fabricius, 1775) and *P. asterius* (Stoll, 1782) were also published in that early period of endeavor to provide a full description of nature and what were perceived as God's works.

A steady stream of taxonomic descriptions followed, in step with the economic conquest of the remaining parts of North America and Eurasia. These provided a sense of the primacy of order, and the security and power of knowledge, for the growing class of people who engaged in this uniquely western activity. In addition, the practice of figuring the name of the author prominently behind the name of a taxon ensured that considerable effort and money was expended in the race to acquire this form of immortality. *Papilio zelicaon* was described by Lucas in 1852 under such circumstances, edging out Boisduval's (1852) *P. zolicaon* by a matter of a few months (Dos Passos, 1962). Obviously new species were exhausted relatively quickly, while the plethora of geographic races in the species of the *P. machaon* group provided an excuse for new names that has not been exhausted to this day. Subspecies names became fashionable around the turn of the last century and many of the older names were subsumed under the very oldest names. The most recent treatment of *Papilio machaon* throughout Eurasia (Seyer, 1974,1976a,1976b,1977) recognizes 36 subspecies in that region alone and synonomizes many more names.

The settlement of western North America in the latter part of the 1800's was integrally associated with many new names. *P. machaon aliaska* was contributed by Scudder (1869), based on material collected by an American lieutenant in a "Russo-American Telegraph Expedition" to Alaska. W.H. Edwards added a number of other names in the same sort of environment. He became wealthy through investments in the expanding railway industry of this period, and his financial security allowed him to play an important role in North American butterfly taxonomy. To the *Papilio machaon* group he contributed the names *P. bairdii* (1866), *P. oregonius* (1876) and *P. nitra* (1884), among others. Several of these taxa are treated in this study.

The discovery and classification of new taxa saw a watershed of sorts in the Victorian era. The abundance of newly collected specimens led to a new understanding of their inexhaustible variation and yet also to a philosophical rift among taxonomists. Darwin's publication of **The Origin of Species** (1859) provided a starting point for this process. By 1883 W.H. Edwards was arguing that criticism of his species designations in the *P. machaon* group was tantamount to a refusal of the teachings of Darwin, which was in turn equivalent to failing to admit the truths of Copernicus. Yet Edwards' names are an example of far greater emphasis on phenetic homogeneity and covariance than on hybridization information. This is particularly noticeable in his treatment of the *P. machaon* populations in the western United States, upon which he bestowed four specific epithets despite knowing that the forms the names referred to were probably all part of the same extended gene pool.

Hagen's (1882) report on the *P. machaon* group was published during the same period as Edwards' work, but showed the opposite tendency to that of Edwards. He looked for and found specimens with character states and combinations that were intermediate between those attributed to all the previously described forms. He concluded that all the North American

species of the *P. machaon* group (excluding *P. indra*) should be considered as local or climatic varieties of *P. machaon*.

Edwards' views prevailed among butterfly taxonomists, in part because David Bruce found that larvae of *P. bairdii* fed on *Artemisia dracunculus* Linneaus (Edwards, 1893 and 1895). This foodplant is a member of the Compositae, rather than the Umbelliferae or Rutaceae that are used by larvae of *P. zelicaon*. Also Bruce found that, in Colorado, *P. bairdii* adults were polymorphic for a yellow wing form which was much more like that of *P. oregonius* and *P. zelicaon* than the mostly black form it had previously been known for. However, Edwards' (1895) taxonomic response was to describe the yellow form from Colorado as yet another new species, *P. brucei*. This conflict between an increasing understanding of evolutionary phenomena such as polymorphism and the need for comprehensible, consistent classifications has continued to provide friction today.

Lord Walter Rothschild dealt with this conflict in a more balanced fashion. He was the epitome of acquisitiveness in the dying days of Victorian thought (Rothschild, 1983), and played a positive role in the systematics of the *P. machaon* group. His curator, Karl Jordan, contributed substantially to putting taxonomic practice in better accordance with evolutionary principles such as geographic differentiation (Mayr, 1955). Rothschild and Jordan consistently and accurately applied the concept of geographic races to their formal recognition of subspecies, and by this contributed to a lasting reduction in the number of taxonomic names used in the *P. machaon* group. Interestingly enough, they saw some specimens from west of Calgary from the same *P. machaon X zelicaon* hybrid populations which piqued my own interest in the group. They continued to use relatively traditional assignments, but remarked on the close resemblance of the black individuals from this area to the black forms of *P. bairdii* (Rothschild and Jordan, 1906).

The 1930's saw a fresh burst of new names proposed for taxa within the *P. machaon* group. Several of these were described from western Canada and Alaska. A. H. Clark (1932) contributed *P. machaon hudsonianus* from the boreal zone of northern Manitoba and Ontario, and *P. machaon petersi* from Alaska. Chermock and Chermock (1937) described *P. machaon* race *avinoffi* and *P. nitra* form *kahli*, both from the Riding Mountains of central Manitoba. McDunnough (1939) described *Papilio machaon dodi* from the prairies of southern Alberta and Saskatchewan. A number of new taxa were also described for the rest of North America during this period, while Eller (1936) produced a major monograph on the races of *Papilio machaon* in Eurasia. Eller (1939) followed this with a shorter treatment of the *P. machaon* group worldwide, in which he, like Hagen (1882), classified all North American taxa except *P. indra* as subspecies of *P. machaon*.

The names *P. machaon avinoffi* and *P. m. petersi* are now generally accepted as synonyms of *P. m. hudsonianus* and *P. m. aliaska*, respectively. *P. m. dodi* is accepted as a valid taxon, but is variously placed as a subspecies of *P. machaon*, *P. bairdii*, or *P. oregonius*. *P. nitra* form *kahli* was elevated without explanation to species status by Wilson (1961) and has generally continued to be used in that manner. Eller's work was rejected in North America, and cited as an example of poorly informed taxonomy (Remington, 1968a).

During the late 1950's, an understanding of the *Papilio machaon* group was placed on a rather different footing. The technique of mating *Papilio* by hand was described in detail by Clarke (1952), and Clarke collaborated in obtaining numerous hybrids in the following years, many of them within the *P. machaon* group (Clarke and Knudsen, 1953; Clarke and Sheppard, 1953, 1955a, 1955b, 1956a; Clarke *et al.*, 1977). Hand pairing became a commonly used

technique in hybridizing even distantly related species within the genus *Papilio*. The papers which Clarke co-authored with Sheppard have been the best studies to date on the genetics of the adult and larval color patterns of various taxa within the *P. machaon* group. They extended their experiments to other species of *Papilio* and produced a number of classic works, including studies on the African mimetic complex of *P. dardanus*. (The understanding of the interactions of genes which was gained from these hybridizing experiments was applied to the prevention of rhesus haemolytic disease in newborn humans, and Clarke was eventually knighted for his work.)

In the United States, Remington also conducted numerous hybridization and rearing experiments on the *P. machaon* group. His first report (1956) on this work was concerned with a collecting trip made to the Riding Mountains to obtain *P. nitra* form *kahli*, but he did not fully publish any of this research. His last report (1968a) included a description of a new species closely allied to *P. zelicaon*. The separation of Remington's *P. gothica* (1968a) was based on the hybrids it produced, as well as slight color pattern and ecological differences from *P. zelicaon*. Sibling species were in fashion in the evolutionary biology and systematics of the time, since they confirmed the primacy of genetic considerations in species definitions. However, Remington's *P. gothica* was soon criticized for a variety of reasons (Clarke and Sheppard, 1970; Shapiro, 1975; Emmel and Shields, 1980) and the only remnant of his concept survived in the form of a subspecific division of *P. zelicaon*.

The name of Remington's (1968a) taxon was later changed to *P. zelicaon nitra* on the basis of hybridization and rearing studies by Fisher (1977). These showed that Edwards' (1884) *P. nitra* was just a dark form of *P. zelicaon*, produced by a single dominant allele. Fisher theorized that the black form had arisen through the introgression of genes from *P. polyxenes*, like Remington's (1956, 1958) earlier thoughts on the origin of *P. nitra* form *kahli* through hybridization between *P. machaon* and *P. polyxenes*.

One of Remington's students, S. Ae, also carried out numerous hybridizations of *Papilio* species. He continued this work for more than two decades in Japan, publishing numerous progress reports and culminating in a major paper on *Papilio* phylogeny (Ae, 1979). He showed that even relatively distant interspecific crosses could produce adults, and many crosses between species within the *P. machaon* group had a reasonable degree of F1 viability. Ae's work is the tip of a veritable iceberg of *Papilio* hybridization studies, carried on by numerous enthusiasts, usually amateur, who rarely if ever publish. Similar situations can be found in saturniid and killifish circles, where the considerable effort to do such work seems to be maintained by a joy derived from the creation of new kinds.

During the last 15 years a substantial number of publications have appeared about the ecology of various members of the *P. machaon* group. These include studies of oviposition behavior (*e.g.*, Wiklund, 1981), larval growth (*e.g.*, Scriber and Feeny, 1979), diapause dynamics (*e.g.*, Sims, 1980) and pupal color determination (*e.g.*, Smith, 1978), among others. Although aimed at an ecological audience, they demonstrate a diversity of potential adaptive mechanisms. A consequence to systematic studies of the *P. machaon* group is that they show how numerous ecological races could have arisen, even within the last century (Shapiro and Masuda, 1980), as variations derived from a single basic gene pool.

There is considerable potential for future research on the *Papilio machaon* group. Clarke and Sheppard (1955b) stated that "It is clear that the Machaon-group provides some of the most suitable material ever investigated in animals for studying the process of speciation in detail, taking into account genetic, ecological and behaviour differences as well as time". I

agree wholeheartedly with this view, in part because the wide variation present within this group of beautiful butterflies makes genetic investigations relatively tractable.

However, study of the *P. machaon* group is also interesting because the variety of hybrid interactions poses conceptual problems in understanding the nature and origin of species. Such hybrid interactions "contrast two views of the species: as a set of populations delimited by genetic barriers to gene exchange; and as a set of populations maintained in a particular stable equilibrium by selection" (Barton and Hewitt, 1985). The appropriateness of study of the *P. machaon* group to an examination of species concepts is illustrated by the fact that Hagen (1882) and Edwards (1883) expressed similar opposing views a century ago.

MATERIALS AND METHODS

Acquisition of Specimens

I examined about 1200 specimens from my own collection, and about 2000 from the collections of the individuals and institutions listed in Table 1. The majority of material from my own collection, including the holotype and a series of paratypes of *P. machaon pikei*, have been deposited at the Canadian National Collection, Ottawa. Voucher specimens have been deposited at the University of Alberta Strickland Museum, as well as locality listings for all specimens examined in the course of this study.

I tried to obtain as many specimens as possible from each of a number of localities located in a rough grid pattern with intervals of 150–200 km across Alberta and northern British Columbia. I collected 20 or more adults from most of these localities, though I had to return to several of them a number of times in different years to do so. These localities comprise much of the geographic survey portion of my study, and are compared to more widely spaced localities in the remainder of western Canada and adjacent United States. I sampled most of the Alberta and northern British Columbia localities several times throughout the summer. Some population samples include adults obtained from larvae collected within about five km of a hilltop locality, as well as specimens from the hilltop itself. They have been distinguished from the wild-collected adults in the sections dealing with foodplant associations. Wherever possible, material taken by other collectors at or near a major locality was included in the morphometric portion of my study.

During the summers of 1980 through 1984 I collected about 650 adults of the *Papilio machaon* group, mostly on hilltops and prominent edges of river banks in Alberta and northern British Columbia. For some samples, I obtained pupae through the mail from other collectors. These included all the samples used in electrophoretic analysis for *P. polyxenes*, as well as most of the material from the *P. polyxenes X machaon* hybrid zone and most of the *P. zelicaon* specimens from southern British Columbia. I also collected about 1800 larvae during 1980–1984, and reared about 450 of these to the adult stage on the same foodplant from which the larvae has been collected. All larval records are listed in Table 14.

Pressed samples of all new foodplant records were identified by Dr. J. G. Packer, Department of Botany, University of Alberta. Records attributed to individuals other than me were identified by those individuals.

Table 1. Sources of specimens examined of the *P. machaon* species group

Names of Curators of institutional collections are listed at ends of entries.

Acorn, J.H., Dept. of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada

Alberta Provincial Museum, Natural History Dept., 12845-102 Ave., Edmonton, Alberta, T5N OM6 Canada (A.T. Finnamore)

Allyn Museum of Entomology, Sarasota, Florida, 326111 U.S.A. (L.D. Miller)

Bird, C.D., Box 165, Mirror, Alberta, T0B 3C0 Canada

British Columbia Provincial Museum, Parliament Buildings, Victoria, British Columbia, V8V 1X4 Canada (R.A. Cannings)

British Museum (Natural History), Cromwell Road, London, SW7 5BD, England (R.I. Vane-Wright)

Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6 Canada (J.D. Lafontaine)

Guppy, C.S., 4120 St. Georges Ave., North Vancouver, British Columbia, V7N 1W8 Canada

Hilchie, G.J., Dept. of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada

Hooper, D.F., Somme, Saskatchewan, S0E 1N0 Canada

Hooper, R.R., Box 205, Fort Qu'Appelle, Saskatchewan, S0G 1S0 Canada

Klassen, P., Box 212, Elm Creek, Manitoba, R0G 0N0 Canada

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Table 2. Descriptions of morphometric characters of adults and larvae of the *P. machaon* group, used in multivariate analyses

Numbering of character states is the same as that used in multivariate analyses.

A. Extent of yellow scaling in cell Cu2, in anal margin of dorsal hindwing (Fig. 2)
1. All except a few yellow scales are restricted to area from inner margin of median dark band to less than halfway to divergence of veins Cu2 and Cu1. (*e.g.*, Fig. 3)
2. Virtually all yellow scales restricted to area between median band and divergence of Cu1 and Cu2.
3. Yellow scales extend past junction of Cu1 and Cu2, but less than halfway between Cu1-Cu2 junction and wing base.
4. Yellow scales extend from median band to more than 3/4 of way to wing base. (*e.g.*, Fig. 2)

B. Shape of pupil in anal eyespot of dorsal hindwing. (Fig. 1)
1. Thin line at lower edge of blue region, connected to wing margin. (*e.g.*, Fig. 1a)
2. Club shaped, in that thinnest portion near margin is less than half the width of thickest portion closer to center of eyespot. (*e.g.*, Fig. 1b, 2, 3)
3. Oblong spot at lower edge of red area, not connected to margin. (*e.g.*, Fig. 1c)
4. Round spot centerd in red area, generally with less than two times as much red above pupil as below it. (Fig. 1d)

C. Extent of black scales between blue and red portions of anal eyespot of dorsal forewing. (Fig. 1-3)
1. Black line extending along less than 1/4 of blue-red boundary. (*e.g.*, Fig. 1a)
2. Black line separating blue from red along between 1/4 and 3/4 of the width of anal eye. (eg. Fig. 1c)
3. Black line separating more than 3/4 of blue from red (boundary line may be wide or narrow).(*e.g.*, Fig. 1b,1d,2,3)

D. Color of hairs on tegula. (Fig. 4 and 6)
1. Virtually all hairs on tegula yellow. (*e.g.*, Fig. 4a-b and 6a-e)
2. Less than half as much yellow on tegula as in typical yellow morph adults but more than about 15%. (*e.g.*, Fig. 4c)
3. Virtually all tegula hairs black. (*e.g.*, Fig. 4d)

E. Extent of yellow scales in basal half of disc of central forewing. (Fig. 5)
1. Yellow scales in more than 50% of area. (*e.g.*, Fig. 5a)
2. Thick streaks or a more general flush to less than 50% of total area. (*e.g.*, Fig. 5b)
3. Few thin streaks or a light sprinkling of yellow scales. (*e.g.*, Fig. 5c)
4. Virtually no yellow scales in basal half of disc of ventral forewing. (*e.g.*, Fig. 5d-e)

F. Extent of yellow scales of postmedian yellow band in apical cell of ventral forewing. (Fig. 5)
1. Postmedian spot large, occupying more area than bordering black scales. (*e.g.*, Fig. 5a-c)
2. Definite patch of diffuse yellow, but occupying less area than black scales. (*e.g.*, Fig. 5d)
3. Virtually no postmedian yellow scales in cell. (*e.g.*, Fig. 5e)

(continued on next page)

Table 2 (continued)

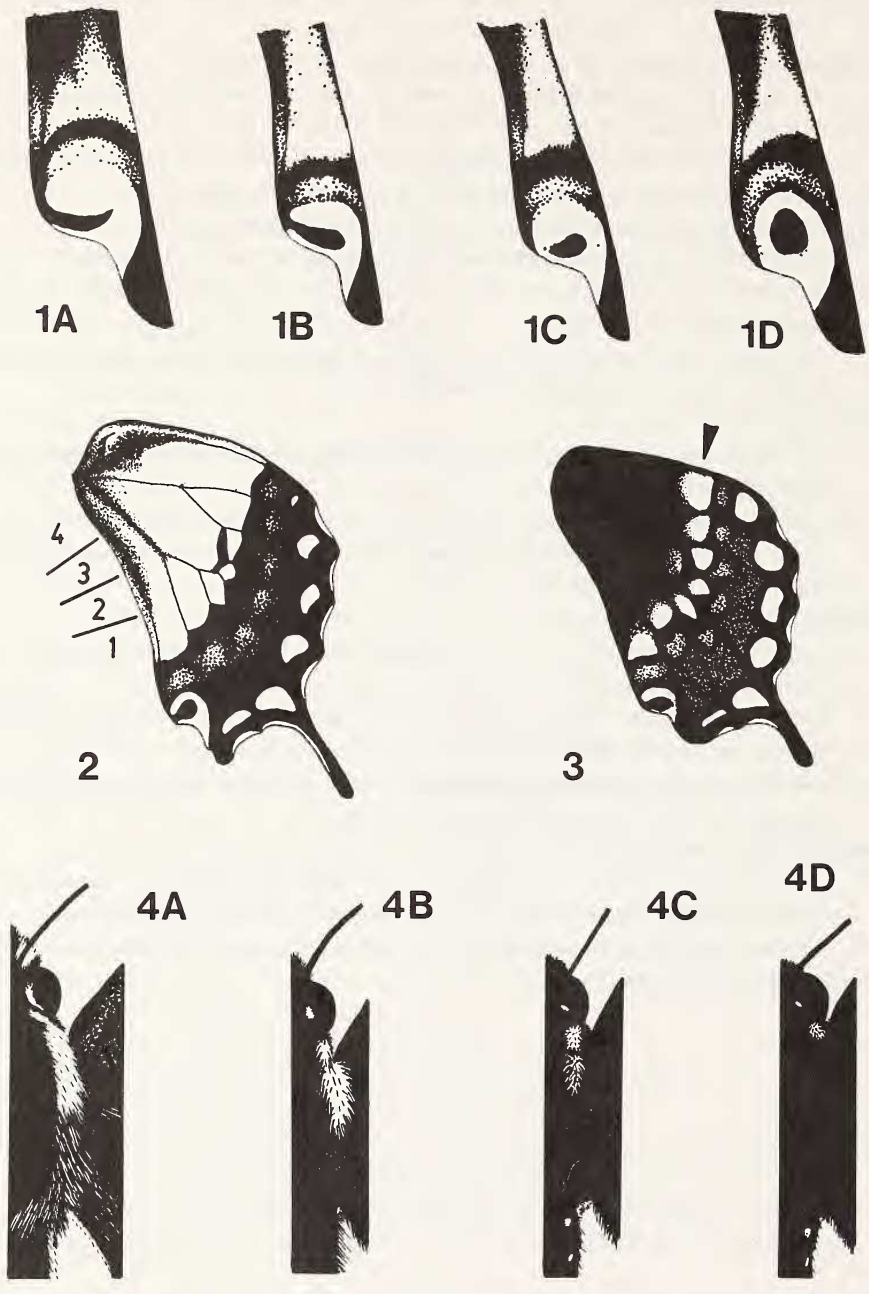
G. Number of cells with orange patch in postmedian area of ventral hind wing. (Fig. 3)
1. No cells with a distinct patch of orange cells on distal side of postmedian yellow area.
2-8. The total number of cells, plus one, which have a distinct patch of orange, up to a total of 7 cells. Postmedian wing cells which are covered in only black scales are assumed to have an orange patch, as in some female *P. polyxenes*.

H. Amount of yellow hair on metathorax below base of hindwings. (Fig. 6)
1. Yellow hairs extend around the ventral part of metathorax. (*e.g.*, Fig. 6a)
2. Substantial patches of yellow hairs on each side of metathorax which do not meet ventrally. (*e.g.*, Fig. 6b-d)
3. All metathoracic hairs black, or at most a very few short yellow hairs restricted to immediate base of wing. (*e.g.*, Fig. 6e-f)

I. Ventral abdominal line. (Fig. 6)
1. All abdominal segments with distinct ventral line of yellow hairs along sagittal plane. (*e.g.*, Fig. 6a)
2-9. The total number of segments, plus one, which do not have a distinct patch of yellow scales or hairs along sagittal line. Start counting from first abdominal segment after thorax, to a maximum of 8.

J. Lateral abdominal yellow. (Fig. 6)
1. Broad band of yellow on each side, extending along length of abdomen (male claspers excluded). (*e.g.*, Fig. 6a-d)
2. Large square lateral spots on some or all abdominal segments, with narrow divisions between spots. (*e.g.*, Fig. 6e)
3. Small round lateral yellow spots on all or most segments, distance separating spots generally greater than width of spots. (*e.g.*, Fig. 6f)

K. Upper abdominal spots. (Fig. 6)
1. All abdominal segments with a distinct pair of subdorsal yellow spots, separated from lateral abdominal band or line of spots (character J., above). (*e.g.*, Fig. 6e-f)
2-9. The total number of segments, plus one, which do not have at least one yellow spot distinct from yellow line.



Figures 1 to 4. Figure 1. Anal eyespot of dorsal hind wing: A, *P. m. aliaska* Mi. 391, Alaska Hwy., British Columbia. B, *P. m. dodi* Nacmine, Alberta. C, *P. zelicaon X machaon* Nacmine, Alberta. D, *P. zelicaon* Wintering Hills, Alberta. Figure 2. Yellow scaling of dorsal hindwing anal margin *P. m. oregonius*, Brewster, WA. Character states for yellow anal scales are numbered beside figure. Figure 3. Ventral hindwing, with location of orange scales *P. p. asterius*, Karlsruhe, North Dakota. Arrow shows postmedian band, which contains orange scales. Figure 4. Dorsal view of thorax, showing tegula: A, *P. zelicaon* yellow morph Wintering Hills, Alberta; B, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; C, *P. p. asterius* Karlsruhe, North Dakota; D, *P. p. asterius* Karlsruhe, North Dakota.

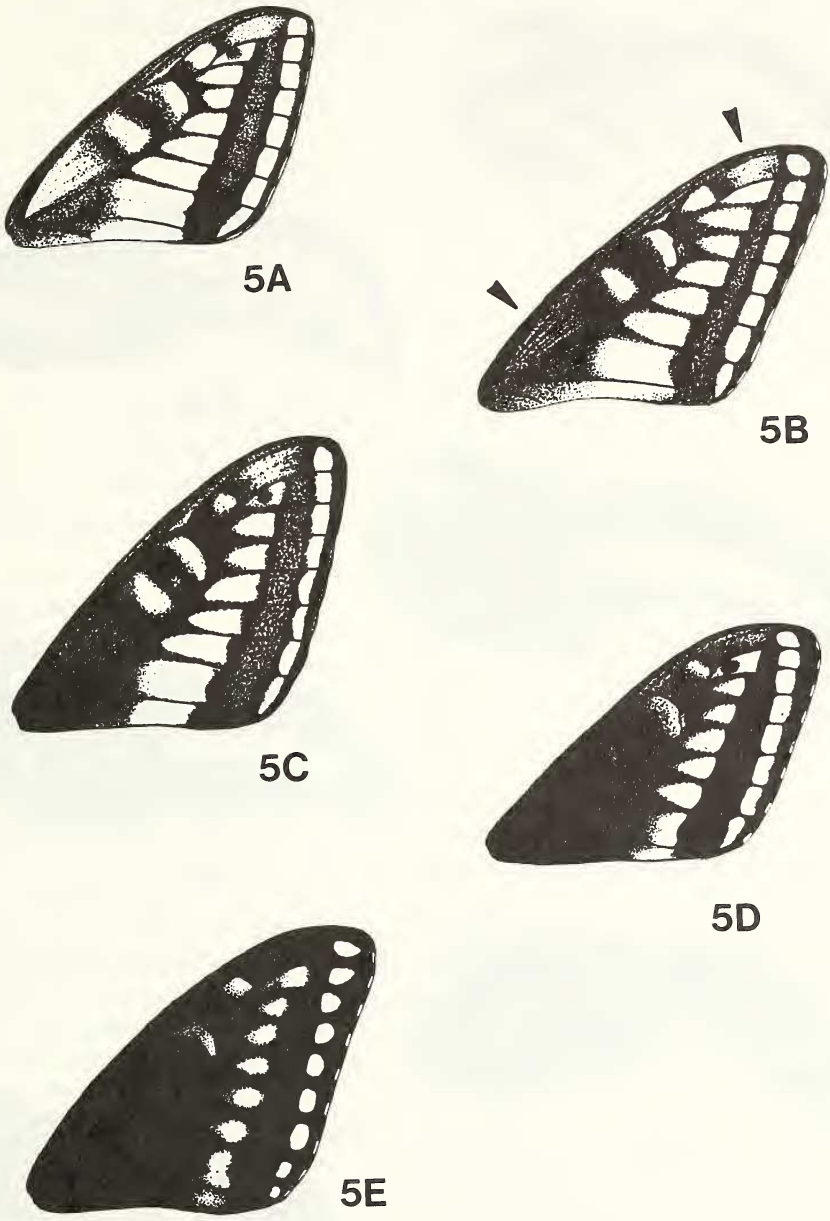


Figure 5. Yellow scales on disc and apex of ventral forewing. Arrows on Figure 5b show location of disc and apical cell: A, *P. m. aliaska* Pink Mountain, British Columbia; B, *P. m. dodi* yellow morph Nacmine, Alberta; C, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; D, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; E. *P. p. asterius* Karlsruhe, North Dakota.

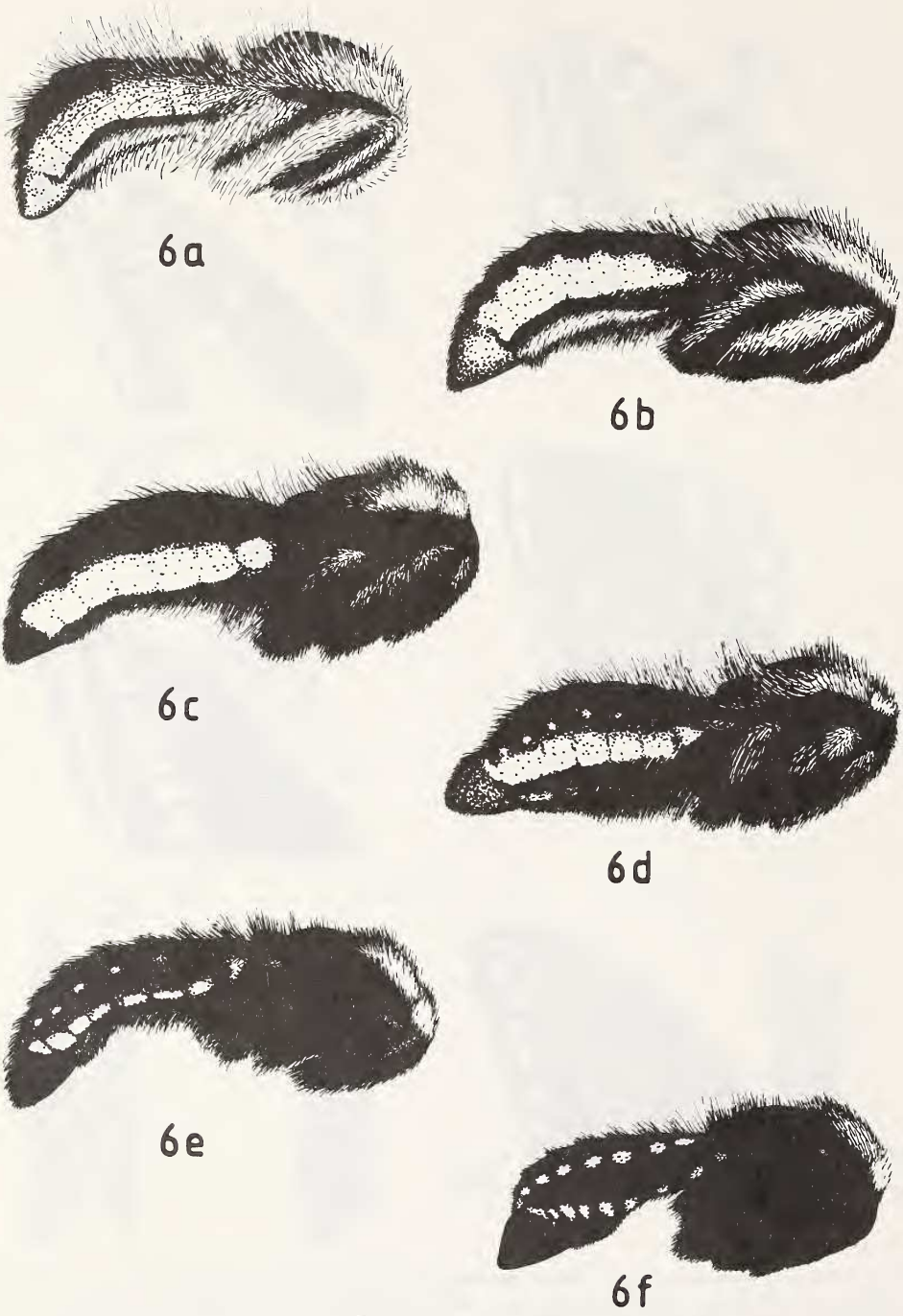


Figure 6. Lateral view of thorax + abdomen. Wings and head have been removed. a, *P. m. aliaska* Pink Mountain, British Columbia; b, *P. m. dodi* yellow morph Nacmine, Alberta; c, *P. zelicaon* yellow morph Wintering Hills, Alberta; d, *P. zelicaon X machaon* yellow morph Bragg Creek, Alberta; e, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; f, *P. p. asterius* Karlsruhe, North Dakota.

Table 3. Names, sources and quantities of proteins, and conditions of gels used in electrophoretic analyses of specimens of the *P. machaon* species group.

Protein		Gel		Homogenate (microliters)	
Symbol	Name	%	pH	Thorax	Abd.
αGPD	α-glycerophosphate DH	9.0	8.9	5	5
G-6-PD	glucose-6-phosphate DH	6.0	8.9	25–30	5–10
IDH	isocitrate DH (NADP)	9.0	8.9	30	15–20
MDH	malate DH	9.0	8.9	5	5
ME	malic enzyme	4.5	8.2	15	30
ODH	octanol DH	9.0	8.9	50	30–50
APK	arginine phosphokinase	7.0	8.9	25	–
Est4 & 5	esterases	7.0	8.9	30	–
Prot1 & 2	general protein	7.0	8.9	20–25	–

Characters Examined

Morphometric characters.— Eleven morphometric characters, defined in Table 2, and illustrated in Figures 1 to 6, were scored for adults used in this study. Individuals were scored against both the written descriptions of character states and a number of standard specimens. Standard and illustrated specimens were labelled as such and are in the Strickland Museum, University of Alberta.

The choice of characters for analysis was made for the following reasons:

1. The characters had been used previously by other workers for distinguishing between species. Those listed by Remington (1968a), were especially useful in this regard, because of the clear manner in which they were defined. This allowed me to relate populations in western Canada to particular species concepts developed elsewhere in North America, and also to test diagnostic structural characters against variation in electrophoretic characters.
2. The characters had to be fast and easy to score by eye, and hence allow accurate processing of numbers of specimens in a relatively short time.
3. There had to be a large amount of variation in character states expressed in the major study area, western Canada. The purpose of this criterion was to maximize the likelihood that useful information would be recorded when a character was scored.
4. Characters were chosen which appeared to vary fairly independently of each other within populations, to maximize the likelihood of sampling the effects of several different genes, and hence of obtaining information of significance to gene flow between populations. I tried to minimize the number of times I scored the presence of the gene for black color, which is known to affect a large area of the adult wings and body (Clarke and Sheppard, 1953, 1955b and 1956a; Fisher, 1977).

I also recorded color of spots on each larva. Spot color was determined by eye and by comparing larvae against each other. I did not use consistently a standard for comparison, but I judge error in assignment of larvae to either a yellow or an orange group to be small. Orange spotted larvae included both the pale orange and bright orange groups delineated by Clarke and Sheppard (1955b). Records were also obtained by contacting lepidopterists who had reared

larvae in western Canada, and by examining published records for spot color for the whole *P. machaon* group.

Electrophoretic characters.— A total of 860 adults of the *Papilio machaon* group were used in electrophoretic analyses. These were frozen live and maintained at -20 C, and most were homogenized within a few weeks of being frozen. However, bands were still readable for whole specimens kept frozen for more than two years.

Tissue for electrophoresis was obtained by dissecting thoracic and abdominal contents from specimens which had been allowed to thaw on ice just before use. The corpus bursa of females was not used, since it may have contained male spermatophores. After tissue had been removed, specimens were pinned through one side of the thorax and mounted in the manner standard for Lepidoptera curation. Each specimen was given a unique number and labelled to allow the morphometric and electrophoretic character states to be correctly associated.

Thoracic and abdominal tissue samples were homogenized separately, each in 0.2 ml homogenizing solution. Homogenate not used immediately was frozen and stored at -20 C in the centrifuge tubes. Most samples gave interpretable bands from frozen homogenate, though esterases and IDH deteriorated the most rapidly when subjected to successive freeze-thaw cycles.

The electrophoretic apparatus used was the same as that described by Rolseth and Gooding (1978), in whose laboratory and under whose direction I did the preliminary work for this study. Some changes have been made in their methods since publication. These include: 1) making the "B" solution with 25.6 ml of 1M H_3PO_4, 5.7 gm Tris and 0.46 ml TEMED, brought up to 100 ml with distilled water; 2) making the homogenizing buffer with 7.0 ml H_2O, 1.0 ml B, .300 gm polyvinylpyrolidine and 40 mg DL-dithiothreitol; 3) forming stacking gels with 20 slots; and 4) sealing the edges of the apparatus with parafilm rather than a plug gel. Also gels were used at pH 8.9 and pH 8.2, using 24 ml and 60 ml of 1M HCl, respectively, in the stock "A" solution. Tissue was electrophoresed at 40 milliamp/gel for 2.0 hours in pH 8.9 gels, and 3.5 hours in pH 8.2 gels. Electrophoresis conditions for the loci used in this study are noted in Table 3; Rf values listed in Tables 6 and 13 refer to electrophoresis performed under these conditions.

Except for the use of $MgCl_2$ rather than $MnCl_2$ as a cofactor for IDH, staining methods are fairly standard applications of recipes available in Shaw and Prasad (1970) or Brewer (1970). Both esterase loci showed much greater activity with α-naphthyl acetate than with β-naphthyl acetate or AS-D-acetate, and were not significantly inhibited by eserine. APK was usually stained with Coomassie blue, since it seemed to be the most common protein that could be resolved by this method in thoraces. The identity of the APK bands was ascertained in several homozygous individuals and the single individual (a male) with an allelic variant, using the staining technique of Gooding and Rolseth (1979).

I stained for a variety of other enzymes, using recipes of Brewer (1970), Shaw and Prasad (1970) and Menken (1980). These included ADH (with ethanol, isopropanol and sorbitol), AO (with benzaldehyde and heptaldehyde), GLUO, GDH, GA-3-PD, GlyDH, LDH, G6PDH, SDH, TO and XDH. In these attempts, bands were either very faint or did not appear.

All except three of the protein loci stained were dimers, while APK and Est4 were monomers, and ME may have been a tetramer. None of the loci included in this study, except possibly APK, were sex linked. Heterozygotes were present in both sexes for all other loci, including G-6-PD, which is frequently sex linked in other taxa.

The genetic inheritance of alleles was not checked through breeding experiments. However, since most of the local populations surveyed had allelic distributions that were at Hardy-Weinberg equilibrium proportions, environmental induction of particular alleles seems unlikely. Also the general distribution of alleles showed an excellent correspondence with morphometric, and ultimately taxonomic, characters.

In any event, my taxonomic conclusions are not strictly dependent on genetic interpretations of protein banding patterns. The bands are treated as equivalent to any other taxonomic character and are more discrete than the character states in my morphometric analysis. An additional advantage of the electrophoretic characters I used is that they probably represent a relatively unbiased selection of loci. The choice of loci for staining was influenced by my ability to obtain bands consistently and my ability to interpret variation in a consistent manner, both of which factors are independent of the morphometric characters measured.

Numerical Analyses

Principal components analysis (PCA) helps to visualize clusters in multivariate data, is relatively assumption-free, and provides a basis for internally consistent, simple comparisons of both individuals and populations. PCA seems to give fairly accurate representation of distances between data points, and has been used successfully in studies of hybrid swarms (Neff and Smith, 1979; Pimentel, 1981). Relatively few characters appear to be required to elucidate patterns of racial variation. Thorpe (1985) showed that patterns with 90% confidence could be obtained from as few as 8–10 characters in grass snakes in Europe. Also, it is easy to relate samples not used in the initial analysis to those that were, by applying factor loadings.

Three major PCAs were applied to an initial group of 728 specimens, almost all of which were from western Canada and particularly Alberta, and all I had available, in early 1984, with complete scores for all morphometric and electrophoretic characters considered in this study. An effort had been made prior to this to obtain a reasonably broad sampling of the different geographic populations and morphotypes known from the region, including those described by other authors. One PCA was performed on only the morphometric characters, one on only the electrophoretic characters and one on the combined morphometric and electrophoretic characters together. The same individuals were used in all three PCAs, to give a more meaningful basis for comparison of variation in character patterns. Then the factor loadings were applied to individuals which could only be completely scored for one of the two main character suites.

Discriminant function analysis (DFA) was applied to subgroups where PCAs did not give clear indications of the number of species in a region or the nature of distinctions among them. DFA was applied to reared adults obtained from southern and south-central Alberta, where adults from different major populations showed only slight separation into the major groups distinguished in other regions. Discriminations were based on the different foodplants, on which larvae were collected. DFA was also applied to the geographically separated subspecies of *P. machaon*, to give an assessment of the accuracy of identification of specimens.

All work for this section of the study was carried out with the Midas statistical package (Fox and Guries, 1976) on the Amdahl computer system at the University of Alberta. The principal component function was used only with the "unscaled" option in this package. The 11 morphometric characters were scaled before PCA or DFA, to make their ranges of variation equivalent. Scaling factors and PCA/DFA loadings are included in Tables 12 and 13. Electrophoretic character scores were not scaled, since these were already recorded in a manner

that gave equivalent weights to each character.

Electrophoretic characters were scored one allele at a time, for each butterfly. Each allele known from my work on the *P. machaon* group was considered a character with three character states and scored: 1), if the allele was absent; 2), if it was present with another allele at that locus; and 3), if it was present in the homozygous state. Of the 42 electrophoretic characters, only a small proportion were significant to the scores on the first few principal component axes. The APK locus was not used in PCA, because there was only one variant in 728 individuals.

An alternative method for scoring electrophoretic characters is used in some numerical analyses (Mickevich and Mitter, 1981; Buth, 1984), with each locus a character, and each allele coded on the basis of its relative mobility. This method was rejected because it does not allow distinction between an individual homozygous for a particular allele, and an individual heterozygous for two alleles located an equal distance on either side of the homozygous allele. This situation occurred frequently at the G-6-PD locus.

Electrophoretic data were also analysed using the Biosys-1 package of Swofford and Selander (1981). Allele frequencies, heterozygosity indices and tests for Hardy-Weinberg proportions were calculated. All individuals with partial electrophoretic information were used, giving a total sample size of 860.

Hardy-Weinberg equilibrium measures provided tests of gene pool homogeneity, and complemented the multivariate clustering techniques. First, the entire sample for a region was tested as a whole before being divided into major groups which might be different species. If the subsets were much closer to equilibrium after the subdivision, this was considered evidence of a significant degree of gene flow within but not between the subgroups. Excess homozygosity may be due to other factors as well, such as the presence of null alleles or temporal and spatial variation within samples. I consider these possibilities unlikely in the context of this study, since the occurrence of excess homozygosity coincided fairly well with taxonomic expectation.

Taxonomic Interpretation and Conventions

I view species concepts as a balance between practicality and meaningfulness. Strict definitions can be established, but they may not distinguish populations of biological relevance. Alternatively, if a species concept is particularly vague or difficult to apply in practical situations, then its potential biological meaningfulness is of little use. Both practicality and meaningfulness should be assessed in terms of the reason for naming species, which is the identification of organisms in a way that allows the user of the name to efficiently communicate information about their relationships with other organisms.

Some taxonomists, for example Blackwelder (1967), view species recognition as a sort of learned trade which cannot be precisely characterized or defined. Here species are kinds of primary concepts. Understanding how to interpret certain kinds of information becomes a matter of developing a sense of similarity relations and applying it in a manner sanctioned by experienced peers. This part of taxonomic training thus involves the transfer among individuals of a conceptual paradigm, in the sense of Kuhn (1970).

However, the uses of systematics are primarily scientific, and there is a need to make its operations repeatable, quantifiable and testable. Most systematists have acknowledged that species tend to be clusters of like individuals, and many of them have focussed on this aspect. Even workers whose main research objectives are in elucidation of evolutionary mechanisms may begin their discussion of species by referring to them as "discontinuous arrays" (Dobzhansky *et al.*, 1977:166). However, some systematists treat species as phenetic covariance

clusters, and de-emphasize reference to reasons for the existence of these clusters. Examples include Ehrlich (1961), who identifies species as relatively arbitrary groups of organisms delineated by overall character similarity, or Neff and Platnick (1981:12), who characterize species as "the smallest detected samples of self-perpetuating organisms that have unique sets of characters". This view appears strongly influenced by the desire to make the process of distinguishing species as tractable as possible, particularly in terms of mechanical simplicity.

Other taxonomists emphasize the process perceived to maintain distinctions between species and unity within species, perceiving gene exchange as the characteristic that makes such a group of organisms a biologically coherent entity. A widely accepted definition of this type is that of Mayr (1969), who defines species as "groups of interbreeding natural organisms that are reproductively isolated from other such groups". However, species descriptions based on hybrid sterility are in some ways as arbitrary as species descriptions based on phenetic clustering, since the degree of hybrid fertility which is accepted before a specific distinction is recognized is itself an arbitrary procedure. One way of dealing with the latter objection has been to characterize different populations as species only if they exhibit 100% hybrid sterility (*e.g.*, Key, 1982). Unfortunately, this definition is so broad that many phenetically distinctive groups of organisms presently recognized as belonging to different species would have to be combined if the definition were rigorously applied.

The attempt to make the process of species recognition more objective thus seems to have led in two major directions: 1), grouping by phenetic covariance; or 2), by interbreeding data. However, grouping on the basis of either data type alone can lead to the absurd extreme of operationalism, in which a definition is conceived as no more than a corresponding set of operations (Hull, 1968). The main fault of operationalism is that it emphasizes practicality in the application of a definition, but restricts the flexibility and general usefulness of the definition.

The history of classification of the *P. machaon* group provides examples of both kinds of operationalism. W.H. Edwards' names are an example of an overemphasis on morphotypes, relative to hybridization information. On the other hand, Hagen's (1882) taxonomic conclusions show an overly strict adherence to the interbreeding criterion of his species concept; thus, he fell into the same trap of operationalism that reduced the value of Edwards' work.

Considering the ecological and genetic complexity of the *Papilio machaon* group, one should not expect sytematic research to have simple taxonomic consequences. I use numerical methods in a predominantly descriptive manner, to characterize the pattern of phenetic variation within and between populations. As in most taxonomic work, there is a need to distinguish variation at the level of local populations, geographic races and species. Geographic patterns of variation were first examined within major character suites, such as structural and electrophoretic characters, and then compared among suites. Finally, these patterns of variation were loosely interpreted in terms of current species concepts, especially through inferences of gene flow and the maintenance of identity in time and space.

Recognition of subspecies is somewhat more arbitrary. My main criterion for formally recognizing a differentiated series of populations or an ecological race as a subspecies is that 75% or more of the specimens can be distinguished without the aid of locality labels (*cf.*, Mayr, 1969). The main reason for using subspecies names is to relate my own findings to previous work, much of which has been couched in terms of description of new specific and subspecific taxa.

Since subspecies are preeminently geographic divisions of species, the former should be at least parapatric, with intermediates occurring along only a relatively narrow zone. Phenetic homogeneity within a subspecies should be quite high compared to that within zones of intergradation. Although most subspecies have been described on the basis of structural characters, ecological characters are also important indicators of substantial genetic distinctions.

The main difficulty in classifying populations and individuals of the *P. machaon* group from western Canada is that in some regions groups of individuals seem like genetically distinct entities in sympatry, while in other areas extensive hybridization occurs. In general, this difficulty is dealt with by continuing to recognize populations as separate species only if areas of sympatry without hybridization are much more extensive than areas in which substantial hybridization occurs. Examples in the *P. machaon* group are discussed in detail in the section on diagnosis of adults and ranking of taxa.

Populations composed predominantly of hybrid individuals were given names which reflect such hybrid origins. Since the International Code of Zoological Nomenclature (1985) does not provide rules for hybrid names, I follow the International Code of Botanical Nomenclature (1983), and more general guides in taxonomy such as Schenk and McMasters (1956). However, the convention of ordering parental names by the sexes which contributed to the hybrid swarms is not useful for the *P. machaon* group. Instead, the species epithets of the parental species are listed, with an "X" between them, so the first epithet indicates the species most similar to the majority of hybrid specimens.

I use form names as little as possible, because they have suffered from considerable uneveness of usage (*e.g.,* Scott, 1981) and have a limited communication value. A better alternative would be to concentrate on distinguishing genes and alleles, as Clarke and Sheppard did in the 1950's with polymorphisms in the *P. machaon* group.

CLASSIFICATION AND RECOGNITION OF TAXA

The taxonomic conclusions of the present study are presented before the supporting data, because I propose several changes to the systems of names which have been applied previously to the *Papilio machaon* group. To simplify presentation of data in succeeding sections, my system is summarized in the present section. Detailed reviews of characteristics of the included taxa follow, and are discussed in succeeding sections, which deal with evolutionary hypotheses.

Summary of Taxonomic Assignments

The following list is based on Miller and Brown (1981), and summarizes the disposition of all scientific names applying to the *P. machaon* group in western Canada and Alaska. It includes type localities, as well as names applying to populations which are found, or have at some time been considered to have been found, in the study area.

P. machaon Linnaeus, 1758:462. Type locality(TL)-Sweden.

a. *P. m. aliaska* S.H. Scudder, 1869:407. TL-Nulato, Alaska.
=*joannisi* R. Verity, 1907:pl.10, Fig. 17. TL-Nulato, Alaska.
=*petersii* A.H. Clark, 1932:8–9. TL-Kuyukok River, Alaska.

b. *P. m. bairdii* W.H. Edwards, 1866:200. TL-"Arizona", restricted to Fort Whipple, Arizona, by Brown (1975).

=*brucei* W.H. Edwards, 1895:239. TL-"Colorado", restricted to Glenwood Springs, Colorado, by Brown (1975).

c. *P. m. oregonius* W.H. Edwards, 1876:208. TL-near The Dalles, Oregon (neotype locality is at Hepner, Oregon [Brown, 1975]).

d. *P. m. hudsonianus* A.H. Clark, 1932:6–7. TL-Kettle Rapids, Manitoba.

e. *P. m. dodi* J. McDunnough, 1939:216–217. TL-Red Deer River, 50 miles N. E. of Gleichen, Alberta (probably near Dorothy [Kondla, 1981]).

f. *P. m. pikei* F.A.H. Sperling. NEW SUBSPECIES. TL-Dunvegan, Alberta.

P. zelicaon Lucas, 1852:136. TL-"California".

=*nitra* W.H. Edwards, 1883:162–163. TL-Judith Mts., Montana.

=*gothica* C.L. Remington, 1968:2–5. TL-Gothic, Colorado.

=ab. *mcdunnoughi* J.D. Gunder, 1928:162. TL-Waterton Lakes, Alberta.

P. zelicaon X machaon NEW HYBRID MORPH

P. polyxenes Fabricius, 1775:444. TL-"America", restricted to Cuba by Rothschild and Jordan (1906).

a. P. p. asterius Stoll, 1782:194. TL-New York, Virginia and Carolina.

P. machaon X polyxenes NEW HYBRID MORPH

=*avinoffi* F.H. and R.L. Chermock, 1937:11–12. TL-Whirlpool River, Riding Mts., Manitoba.

P. polyxenes X machaon NEW HYBRID MORPH

=*kahli* F.H. and R.L. Chermock, 1937:12-13. TL-Riding Mts., Manitoba.

Papilio machaon pikei, new subspecies

Of the five major sections of *P. machaon* which occur in western Canada, four were described many years ago. The fifth occurs exclusively within the Peace River region, and appears to have been collected once (Llewllyn Jones, 1951) before being rediscovered by E.M. Pike and me in 1980. The Peace River race of *P. machaon* is ecologically distinct from *P. m. aliaska* and *P. m. hudsonianus*, and is geographically disjunct from *P. m. dodi* and *P. m. oregonius*. Although very similar in morphometric and electrophoretic features to the other subspecies of *P. machaon* in western Canada, it is as different from each of these as they are from each other. In order to facilitate discussion about the evolution of this race, it is described below. All measurements are based on specimens used in the principal components analyses in the following section.

Description.— *Adult* (Plate 1, e-f). *Male* (Plate 1, e). Mean forewing length, from base at thorax to apex, 40.8 mm (range 36.5–47.0). Dorsal hindwing with yellow scales extended over proximal portion of wing almost to base, except in cell Cu2, latter with yellow scales confined to postmedian region. Black pupil of dorsal hindwing eyespot along lower edge of red scales and connected to margin of wing. Pupil club-shaped or narrow line. Blue and red scales of eyespot separated by few or no black scales. Basal half of ventral forewing disc covered by yellow scales. Postmedian area of ventral hindwing of most specimens with distinct patch of orange scales in two or fewer cells. Thorax covered by long yellow hairs ventral to wings. Ventral side of abdomen with yellow hairs on all segments. Broad yellow lateral band on abdomen, extended over claspers. Subdorsal spots above lateral abdominal band in few specimens. *Female* (Plate 1, f). Like male, but larger (mean forewing length = 42.6 mm, range = 39.5–45.5), and with more rounded forewing.

Immatures. Eggs, larvae and pupae very similar in all stages to those of *P. m. oregonius* (see Perkins, *et al.*, 1968 for photographs) and to *P. m. dodi*. Fifth instar larvae with segmental spots orange or yellow, but most individuals with orange spots. Background color of mature larvae from flat blue-green to bright emerald green. Pupae either mottled brown or green, but not mixture of brown and green as in some specimens of *P. m. aliaska*. Larval foodplant *Artemisia dracunculus*, on warm, dry, eroding exposures.

Type series. Abbreviations: **f** = female, **m** = male, *Ad* = *Artemisia dracunculus*, E4# = F.A.H. Sperling electrophoresis number, CNC = Canadian National Collection. All reared specimens have pupal shell and some have fifth

instar larval skin attached to card below specimen. Pupation and emergence dates are omitted in the following list. Seventy eight paratypes have been deposited in public institutions, and 20 remain in the personal collection of E.M. Pike. Sites of deposition are listed in brackets behind each entry.

Holotype: male. Canada, Alberta; Dunvegan (s. Fairview); June 14, 1981; F.A.H. Sperling; [on dry, grassy, south-facing slopes above Peace River] (CNC).

Allotype: female. Canada, Alberta; Dunvegan; June 22, 1982; F.A.H. Sperling; e4# 546 (CNC).

Paratypes. 2**f**, 6**m**: Canada, B.C.; Attachie; larva coll. Aug 9 '81; F. Sperling; on *Ad*; e4# 521–526,528,529 [all emg. 1983], (CNC). 2**f**, 1**m**: Attachie, British Columbia; 35 km W. Ft. St. John; larva coll. Aug. 9, 1981; on *Ad*; [all emg. 1982]; F. Sperling (CNC). 1**m**: Attachie, British Columbia; 35 km W. Ft. St. John; larva coll. July 9, 1981; on *Ad*; F. Sperling (CNC). 1**m**: Taylor, B.C.; July 3 '80; F. Sperling (CNC). 1**f**: larva on *Ad* at Taylor, B.C. on Aug. 18, 1980; [emg. 1981]; F.A.H. Sperling; e4# 627, (CNC). 1**f**: Canada, B.C.; Taylor; larva coll. July 8 '82; F. Sperling; on *Ad*; e4# 439 (CNC). 3**f**, 6**m**: Canada, B.C.; Taylor; June 21, 1982; F. Sperling; including e4# 6,7,55,56,59,124,128,395; (British Columbia Provincial Museum: e4# 59[f],124[m]. American Museum of Natural History: e4# 6[m],55[f]. United States National Museum: e4# 56[m], 128[f]. remainder to CNC). 1**f**, 2**m**: Canada, B.C.; Taylor; July 8, 1982; F. Sperling; e4# 10,31,140; (CNC: e4# 31[m]. British Museum [Natural History]: e4# 10[m],140[f]). 2**f**: Clayhurst Ferry, B.C.; larva on *Ad*; Aug. 17 '80; emg. 1981; F.A.H. Sperling; including e4# 117; (CNC: e4# 117[f]. Allyn Museum of Entomology: 1f). 3**m**: Clayhurst Ferry, British Columbia; larva coll. Aug. 9, 1981; on *Ad*; emg. 1982[2] & 1983[1]; F.A.H. Sperling; including e4# 519, (CNC). 4**f**, 7**m**: Canada, B.C.; Clayhurst Ferry; larva coll. Aug. 16 '82; F. Sperling; on *Ad*; emg. 1983; e4# 504,507,508,511–513,515–518,520, (Allyn Museum of Entomology: e4# 507[m]. remainder to CNC). 5**m**: Alberta, 5 km NW Highland Park; June 14, 1981; F. Sperling; e4# 115,116,676,678,679, (CNC). 5**m**: Canada, Alberta; Highland Park; 35 km w Fairview; June 9, 1982; F.A.H. Sperling; e4# 41,42,43,44,45, (Alberta Provincial Museum: e4# 41,43. CNC: e4# 42,44,45). 9**m**: Canada, Alberta; Highland Park; 20 mi. W. Fairview; June 12, 1982; Ted Pike, (CNC). 5**m**: Canada, Alberta; Highland Park; 20 mi. W. Fairview; June 13, 1982; Ted Pike, (Pike). 1**m**: Dunvegan, Alberta; larva on *Ad*; Aug. 16, 1980; emg. 1981; F.A.H. Sperling, (CNC). 1**f**: Canada, Alberta; Dunvegan; June 14, 1981; F.A.H. Sperling, (University of Alberta Strickland Museum). 1**f**, 2**m**: Alberta, Dunvegan; June 14, 1981. T. Pike, (Pike). 1**f**: Canada, Alberta; Dunvegan; larva coll. Aug. 15, 1982; F.A.H. Sperling; on *Ad*; emg. 1983; e4# 438, (CNC). 3**m**: Canada, Alberta; Dunvegan; June 22, 1982; F.A.H. Sperling; e4# 142,150,547, (University of Alberta Strickland Museum: e4# 150[m]. remainder to CNC). 1**f**: Dunvegan, Alta.; 30 VI 85; coll. by E.M. Pike; (Pike). 1**m**: EX OVA; Dunvegan, Alta.; 18 VI 85; coll. by E.M. Pike; (Pike). 4**m**: 10 mi. S.E. Fairview; Alberta; 17 June 1981; coll. by E.M. Pike; (Pike). 2**m**: 10 mi. S.E. Fairview; Alberta; 20 & 22 June 1981; coll. by E.M. Pike; (Pike). 1**f**, 2**m**: Canada, Alberta; 10 mi. S.E. Fairview; June 22, 1982; Ted Pike; (Pike). 1**f**: 10 mi. S.E. Fairview; Alta., 20 VI 85; coll. by E.M. Pike, (Pike). 1**m**: Canada, Alberta; Peace R. area, Camp Island; 22 mi. E. Dunvegan; F.A.H. Sperling; larva on *Ad* on Aug. 15, 1980; [emg. 1981], (CNC). 1**f**: larva on *Ad*; at Peace R. (town), Alberta; on Aug. 15, 1980; emg. 1981; F.A.H. Sperling; e4# 625, (CNC). 4**m**: Alberta, Peace River (town); June 10, 1981; F. Sperling (CNC). 2**m**: Canada, Alberta; Peace River (town); June 13, 1981; F.A.H. Sperling; e4# 114,681, (CNC). 1**m**: Canada, Alberta; Kleskun Hills; 25 km n.e. Grande Prairie; June 19, 1982; F.A.H. Sperling; e4# 394, (CNC). 1**f**: Canada, Alberta; Kleskun Hills; e. Grande Prairie; larva coll. Aug. 12 '81; F.A.H. Sperling; on *Ad*; emg. 1983; e4# 437, (CNC).

Derivation of subspecific epithet.— It is a pleasure to name this subspecies after E.M.(Ted) Pike, who has resided in the Peace River region from 1979 to 1985, and has given me much help and encouragement during the past 15 years.

Distinguishing features.— Approximately 75% of individuals of *P. m. pikei* can be correctly distinguished from those of other subspecies of *P. machaon*. Features which distinguish this subspecies are discussed at greater length in the following chapters. Adults of *P. m. pikei* resemble those of *P. m. oregonius* in general maculation and size, but most are distinguished by the more narrow, connected eyespot. *P. m. aliaska* adults resemble those of *P. m. pikei* markedly in maculation, but are separated by larval foodplant, preference for alpine habitat, and smaller size (mean forewing length = 37.5 mm for males, 40.3 mm for females). Though the range of *P. m. pikei* extends in isolated populations to within 25 km of *P. m. aliaska*, at Hudson Hope, there is no evidence of any increased similarity of these two subspecies in the area. *P. m. hudsonianus* adults are separated by preference for boreal forest habitats and a much higher frequency of subdorsal abdominal spots. *P. m. dodi* is easily distinguished from *P. m. pikei* by the greater amount of black scales and hairs, especially on the ventral forewing disc and ventral side of the thorax.

P. m. pikei has the same larval foodplant as the southern subspecies of *P. machaon*, but shares several morphometric and electrophoretic similarities with the northern subspecies. For these reasons, as well as its geographic range, *P. m. pikei* is important in illustrating the

previously unrecognized link between these taxa.

Range.— *P. m. pikei* is composed of a series of populations distributed along approximately 500 km of the Peace River, in northeastern British Columbia and northwestern Alberta. It also occurs at the Kleskun Hills badlands, northeast of Grande Prairie, Alberta. The range of *P. m. pikei* may have once extended farther westward along the Peace River. A specimen in the University of British Columbia collection, which is labelled "Findlay, B.C.", may be from Findlay Forks, 110 km west of Hudson Hope. However, the populations along this part of the Peace River may now be extinct, since it was flooded to form Williston Lake in the late 1960's.

Key to Adults of *P. machaon* Group in Western Canada

The following key is based on color pattern and habitat information. Electrophoretic characters are not used.

1 Black scales on disc of dorsal hindwing (DHW) restricted to basal half (Fig. 2); side of abdomen with broad, yellow, longitudinal band and in some specimens with rounded spots above it (Figs. 6a-d) 2

1′ Black scales extended over more than half of DHW disc (Fig. 3); side of abdomen with only series of square or rounded segmental yellow spots (Figs. 6e-f) 9

2 (1) *All of the following character states*: Black pupil in anal region of DHW connected to margin (Figs. 1a-b,2,3); yellow scales over most of ventral forewing (VFW) disc (Fig. 5A); yellow hairs extended around ventral part of metathorax (Fig. 6a); yellow scales extended over more than 80% of male claspers (Fig. 6a).
Or no more than one of following: Anal pupil unconnected to margin but flattened and at bottom of red area (Fig. 1C); yellow scales in VFW disc restricted to thick yellow streaks or general flush extended over more than quarter of disc (Fig. 5B); yellow scales extended over only 50–80% of male claspers (Fig. 6b) ..... *P. machaon* Linneaus (Plate 1) 4

2′ Not as above 3

3 (2′) *All of following*: Anal pupil round and centered in red area (Fig. 1D); red and blue areas of anal eyespot more than 3/4 separated by black scales (Figs. 1b,1d,2,3); disc of VFW with at most few thin streaks or light sprinkling of yellow scales (Figs. 5c-e); metathorax with yellow hairs from both sides not in contact ventrally (Figs. 6b-d); without distinct yellow spots above lateral abdominal band (Figs. 6b-c); less than 50% of male claspers covered by yellow scales (Figs. 6c-d).
Or no more than one of following: Anal pupil large, round and centered if connected to margin (Fig. 2) or small and oval at bottom of red area if unconnected (Fig. 1C); red and blue areas of anal eyespot separated between 1/4 and 3/4 of full width by black scales (Fig. 1C); disc of VFW with thick streaks of yellow or a general flush over less than 1/4 of the disc (Fig. 5B); some distinct yellow spots above lateral abdominal band (Fig. 6d); yellow scales over 50–80% of male claspers (Fig. 6b) ..... *P. zelicaon* Lucas (Plate 2g-h)

3′ Not as above: most specimens with club-shaped pupil connected to margin;

also most specimens with two or more of character states intermediate between extremes of *P. machaon* and *P. zelicaon* as defined above, rather than combination of extreme states 7

4 (2) Found near dry grasslands or eroded clay banks in hot habitats; large (FW length usually 40 mm or more in males); forewing apices pointed or not, with distal margin convex or concave; most specimens with yellow scaling of DHW anal cell Cu2 extended close to or beyond divergence of veins Cu1 and Cu2 (Fig. 2: character states 2–4); few specimens with abdomen with spots above lateral band 5

4′ Found in forested boreal regions or on alpine tundra in cool habitats; smaller (FW length usually less than 40 mm in males); forewing apices of most specimens rounded, with convex outer margin (Fig. 5A); yellow scaling of DHW anal cell Cu2 in most specimens restricted to distal 1/4 (Fig. 2: character state 1); abdomen with or without yellow spots above lateral band 6

5 (4) Found in southern and central B.C. Interior, during April to September; anal pupil of eyespot connected to margin in most specimens, but club-shaped rather than flat line; separation between blue and red areas of anal eyespot various; with substantial amount of orange in two or more cells of VHW postmedian band; most specimens with forewing apices pointed, with concave distal margin; (Note: a few summer generation *P. m. dodi* from the southern Alberta and Saskatchewan prairies key out here) ..... *P. machaon oregonius* (Edwards) (Plate 1g-h)

5′ Found in Peace River region of northeastern B.C. and northwestern Alberta, during June and early July; anal pupil of many specimens flat rather than club shaped; most specimens with very little black separation between red and blue in anal eyespot; most specimens with substantial amounts of orange in only one or no cell of the VHW postmedian band; forewing apices pointed or rounded ..... *P. machaon pikei* Sperling (Plate 1e-f)

6 (4′) Found in Alaska, Yukon, western Northwest Territories, and northern British Columbia, most specimens on alpine tundra; DHW anal pupil in form of thin line, at bottom of red area, and connected to margin (Fig. 1A); red and blue areas of anal eyespot with no or very little black separation (Fig. 1A); no spots or in few specimens one or two spots on abdomen above lateral band ..... *P. machaon aliaska* Scudder (Plate 1a-b)

6′ Found in boreal forest from Alberta to northern Quebec; DHW anal pupil in most specimens club shaped; red and blue areas of anal eyespot separated or not by black scales; at least one yellow spot above lateral abdominal band in most specimens ..... *P. machaon hudsonianus* Clark (Plate 1c-d)

7 (3′) Found near dry grassland or eroding clay banks in hot prairie habitats of southern Alberta or Saskatchewan; anal pupil of DHW club-shaped and connected to margin; forewing apex of many specimens pointed, with concave distal margin; hindwing tails of many specimens long, slightly narrowed in middle and curved (Fig. 2); yellow scales in DHW anal cell

Cu2 extended or not beyond divergence of veins Cu1 and Cu2 (Fig. 2: character states 3–4); no distinctly separated yellow spots above lateral abdominal band ..... *P. machaon dodi* McDunnough (Plate 2a-b)

7′ Found in broad range of habitats, but most in southern zones of boreal forest; anal pupil of DHW varied; forewing apex of most specimens rounded, and distal margin straight or rounded; hindwing tails of medium or short length, straight and not constricted in middle (Fig. 3); yellow scales of distal hindwing cell Cu2 in most specimens restricted to distal quarter; less than five yellow spots above lateral abdominal band ..... yellow morph hybrids 8

8 (7′) Found in Manitoba or eastern Saskatchewan *and* with one or more of the following character states: anal pupil on DHW round and centered; disc of VFW with at most light sprinkling or thin streaks of yellow scales; thorax with yellow hair not in contact ventrally and no yellow hairs on ventral midline of first two abdominal segments; male claspers covered over less than 50% of surface by yellow scales ..... *P. machaon X polyxenes*

8′ Found in western Saskatchewan and westward, with any of the following combinations:

A. In predominantly forested habitats and with club shaped, connected pupil.

or **B.** Specimen with between two and five of the following six character states: 1, DHW anal pupil connected to margin or unconnected, flattened and at bottom of red area; 2, Blue and red areas of anal eyespot not separated by black along at least 1/4 of boundary; 3, disc of VFW with yellow scales or thick streaks over at least 1/4 of area; 4, metathorax with yellow hair meeting ventrally; 5, one to five distinct spots above lateral abdominal band; 6, yellow scales over more than 50% of male claspers ..... *P. zelicaon X machaon* (Plate 2c-f)

9 (1′) Found in southern and central Manitoba or southeastern Saskatchewan; postmedian band of VHW with substantial amounts of orange in at least two cells, and all cells in most specimens; distinct yellow spots in two subdorsal rows on at least five and in most specimens on all segments of abdomen 10

9′ Found in southwestern Saskatchewan and south or central Alberta; postmedian band of VHW with substantial amounts of orange in less than six cells (only two or three in most specimens); distinct yellow spots in subdorsal position on abdomen usually absent on at least 2 segments 11

10 (9) Anal pupil of DHW unconnected to margin or club shaped if connected; blue and red areas of anal eyespot fully separated by band of black scales; less than half of hairs on tegula yellow; yellow scales in apical cell of postmedian band of VFW varied; postmedian band of VHW with orange in all eight cells; lower half of side of abdomen with rounded yellow spot on each abdominal segment; yellow spots in subdorsal position on abdomen absent on no more than two segments; less than 10% of male claspers covered by yellow scales; females with markedly reduced postmedian band on DHW, compared to males ..... *P. polyxenes asterius* Stoll (Plate 3g-h)

10′ *All three of following character states*: anal pupil club-shaped and connected to margin; more than 50% of hairs on tegula yellow; apical cell of VFW postmedian band with distinct patch of yellow, but occupying less than half of cell area;
or one or more of the following character states: anal pupil thin line at lower edge of red area, connected to margin; blue and red areas of anal eyespot not completely separated by black scales; apical cell of VFW postmedian band more than 50% covered by yellow scales; postmedian band of VHW with no orange in at least one cell; large square spots or broad band of yellow along lower half of abdomen; yellow spots in subdorsal position on abdomen absent from at least three segments; more than 10% of male claspers covered by yellow scales; females with postmedian band on DHW same width as on males ..... *P. polyxenes X machaon* (Plate 3d)

11 (9′) Anal pupil of DHW round and centered in red area; blue and red areas of anal eyespot fully separated by black scales; male claspers with less than 10% yellow scales ..... black morph of *P. zelicaon* (Plate 3a)

11′ One or more of following character states: anal pupil of DHW connected to margin or low and oval if unconnected; blue and red areas of anal eyespot of DHW not separated by black scales along at least 1/4 of boundary; male claspers with more than 10% yellow scales 12

12 (11′) Found near dry grassland or eroding clay banks in hot prairie habitats ..... black morph of *P. machaon dodi*

12′ Found in predominantly forested habitats ..... black morph of *P. zelicaon X machaon* (Plate 3b-c)

MORPHOMETRIC AND ELECTROPHORETIC CHARACTERS

Characters of Adults

Only a few species within the *Papilio machaon* group are easy to distinguish on the basis of morphometric characters. The most divergent of these is *P. alexanor* Papilio, which has a striped wing pattern and male genitalia unlike the other species of the group (Higgins, 1975), but shares with them an apotypic (derived) larval color pattern and larval foodplant. Diagnostic interspecific distinctions in genitalia are also found in *P. indra* and *P. hospiton*. The remaining five species in the *P. machaon* group are much more similar with respect to adult characters.

The character states traditionally used by systematists to distinguish among *P. machaon*, *P. zelicaon* and *P. polyxenes* are especially difficult to employ, because the variation in color pattern in any one species is paralleled by the other species in other areas. Also, virtually no character states stand on their own, without consideration in combination with other characters. For this reason, I use multivariate statistical methods to provide more reliability in clustering groups of similar individuals, both at the level of populations and species. As well, two character suites were surveyed and compared: one, the traditionally employed color pattern data; and two, new information about enzyme alleles.

Cluster resolution with principal components analysis.— Three principal components analyses (PCAs) were applied to the same 728 individuals using, respectively, morphometric data, electrophoretic data, and both data sets combined. All PCAs gave generally similar orientations of locality samples (Figures 7 and 8).

These samples were then compared with samples from or near the type localities of named populations, which were scored with factor loadings derived from analysis on morphometric data alone (Figure 9). From this comparison, it was clear that in all three principal components analyses the first axis separated most yellow morph populations of *Papilio machaon* (No. 1,2,3,5,12,13,15) from *Papilio zelicaon* (No. 8,9,10,16,17a,18,19), the second axis separated *Papilio polyxenes* (No. 11,17b,20) from the previous two groups and the third axis provided a partial separation of the *P. machaon* cluster. Factor loadings for all three PCAs are included in Tables 12 and 13.

Electrophoretic characters showed a close association between (*P. m. dodi* Figure 7, No. 5) and other *P. machaon* subspecies, while morphometric characters (Figure 8 and 9) indicated a more intermediate position for *P. m. dodi* between *P. zelicaon* and other *P. machaon* subspecies. Populations from the Alberta foothills, such as Bragg Creek, were intermediate in both electrophoretic and morphometric characters. *P. m. oregonius* populations, which have not previously been associated with *P. machaon* in most publications, showed a close association with *P. machaon* on the basis of both character suites.

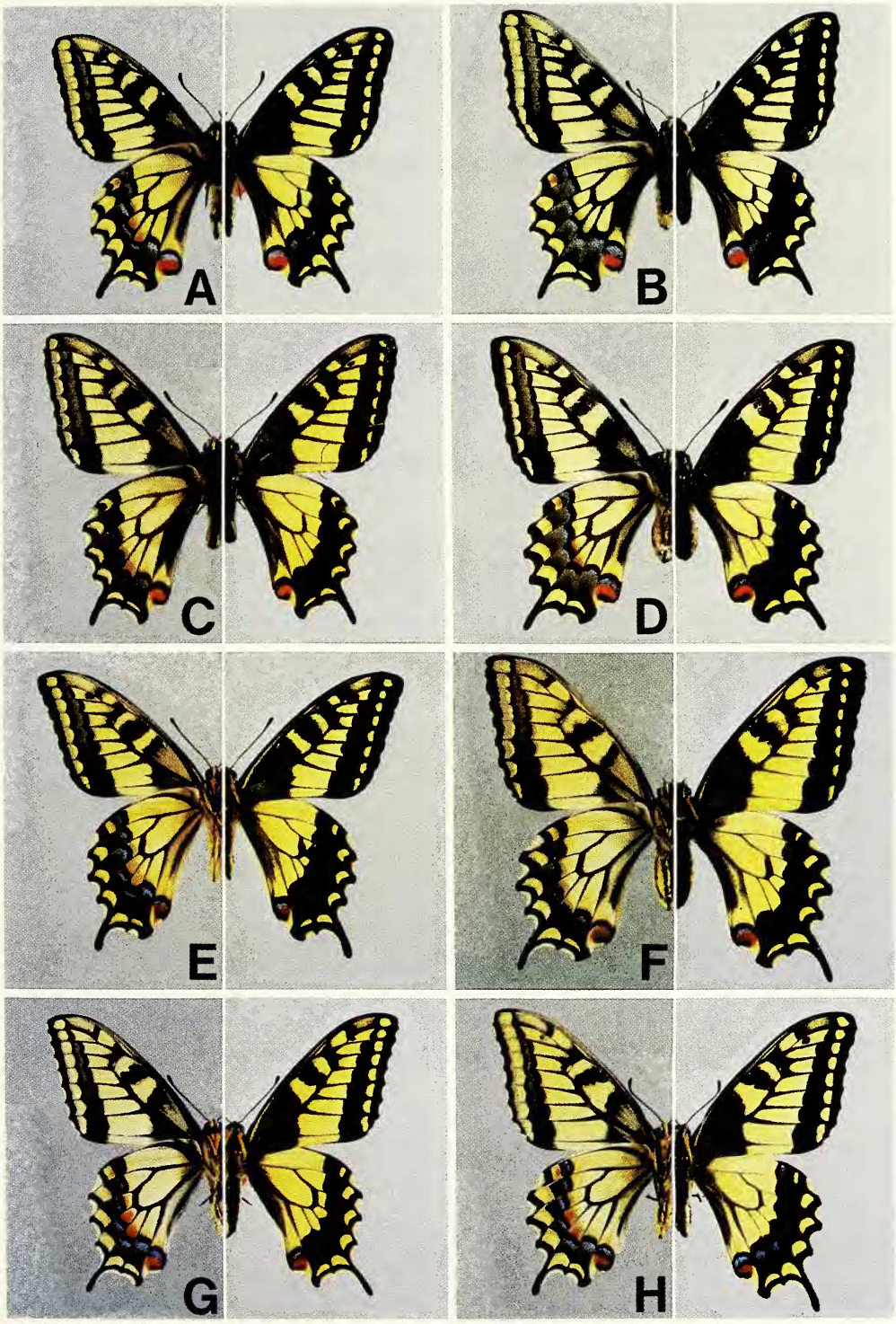
Although the second axis of each of the three PCAs served to separate *P. polyxenes* from both *P. machaon* and *P. zelicaon*, the black morphs associated with populations of predominantly yellow individuals were placed in an intermediate position between them in those analyses which included morphometric data. Electrophoretic characters showed a much closer association between the black and yellow morphs of most populations. The sample size from central Manitoba (No. 14) was relatively small; nonetheless, the single yellow morph specimen showed a close association with *P. machaon* for both character types. The black samples from central Manitoba showed a somewhat closer association with *P. machaon* than with *P. polyxenes* on the basis of electrophoretic characters, and grouped closely with *P. polyxenes* in morphometric characters.

Although plotting entire population samples on the principal component axes served to group most of these with either *P. machaon*, *P. zelicaon* or *P. polyxenes*, the associations of a number of intermediate samples were uncertain. In particular, this procedure did not distinguish between samples which were intermediate because the whole population was intermediate, and samples which contained a mixture of individuals of more than one of the above species. To facilitate such a distinction, the scores of all the individuals within a region or at a locality were plotted as frequency histograms on principal component axes (Figures 12–13). Since there seemed to be regional trends with respect to the frequency of intermediate individuals, the total sample used in the original PCAs was divided into five major regions (Figure 10).

Both morphometric and electrophoretic characters provided a good separation of *P. machaon* from *P. zelicaon* in southern and central British Columbia, as well as in the Peace River region (Figure 12). The few specimens which were intermediate on the basis of either character type grouped with *P. zelicaon* when both character types were considered together. The sample from southern Alberta and Saskatchewan showed a reasonable degree of clustering on the basis of electrophoretic but not morphometric characters, and the low frequency section between these two clusters was shifted toward *P. zelicaon*, with both character suites considered simultaneously.

With samples from the southern Alberta and Saskatchewan region considered separately, it was clear that the frequencies of *P. machaon* and *P. zelicaon* differed markedly by locality (Figure 11 and 15). Specimens collected along high river banks were likely to be more similar

Plate 1. Color pattern of *P. machaon* subspecies. Each specimen has dorsal and ventral views of right wings figured on right and left sides, respectively: a, *P. m. aliaska*, male Mi. 391, Alaska Hwy., British Columbia, July 2, 1972; b, *P. m. aliaska*, female Pink Mountain, British Columbia, *Ex* larva, coll. 17 Aug. 1982, on *Artemisia arctica;* c, *P. m. hudsonianus*, male Thompson, Manitoba, July 2, 1983; d, *P. m. hudsonianus*, female 25 km NE of The Pas, Manitoba, June 14, 1980; e, *P. m. pikei*, male 7 km NE of Hudson Hope, British Columbia, *Ex* larva, coll. 20 Aug. 1984, on *Artemisia dracunculus*; f, *P. m. pikei*, female Dunvegan, Alberta, June 14, 1981; g, *P. m. oregonius*, male Kamloops, British Columbia, *Ex* larva, coll. 27 Aug. 1983, on *Artemisia dracunculus*; h. *P. m. oregonius*, female Kamloops, British Columbia, *Ex* larva, coll. 27 Aug. 1983, on *Artemisia dracunculus*.


A
B
C
D
E
F
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H

Plate 2. Color pattern of *P. machaon, P. zelicaon* and hybrids Each specimen has dorsal and ventral views of right wings figured on right and left sides, respectively. Figure h is reversed and shows left wings: a, *P. m. dodi*, male 11 mi. N of Taber, Alberta, *Ex* larva, coll. 19 Aug. 1981, on *Artemisia dracunculus*; b, *P. m. dodi*, female Drumheller, Alberta, *Ex* larva, coll. 22 July 1981, on *Artemisia dracunculus*; c, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, *Ex* larva, coll. 18 July -7 Aug. 1982, on *Zizia aptera*; d, *P. zelicaon* X *machaon*, female Bragg Creek, Alberta, *Ex* larva, coll. 18 July -7 Aug. 1982, on *Zizia aptera*; e, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, May 31, 1980; f, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, May 31, 1980; g, *P. zelicaon*, male Wintering Hills, 18 km S Drumheller, Alberta. May 24, 1982; h, *P. zelicaon*, female Waterton Park, Alberta. *Ex* larva, coll. 19 Aug. 1981, on *Lomatium dissectum*.

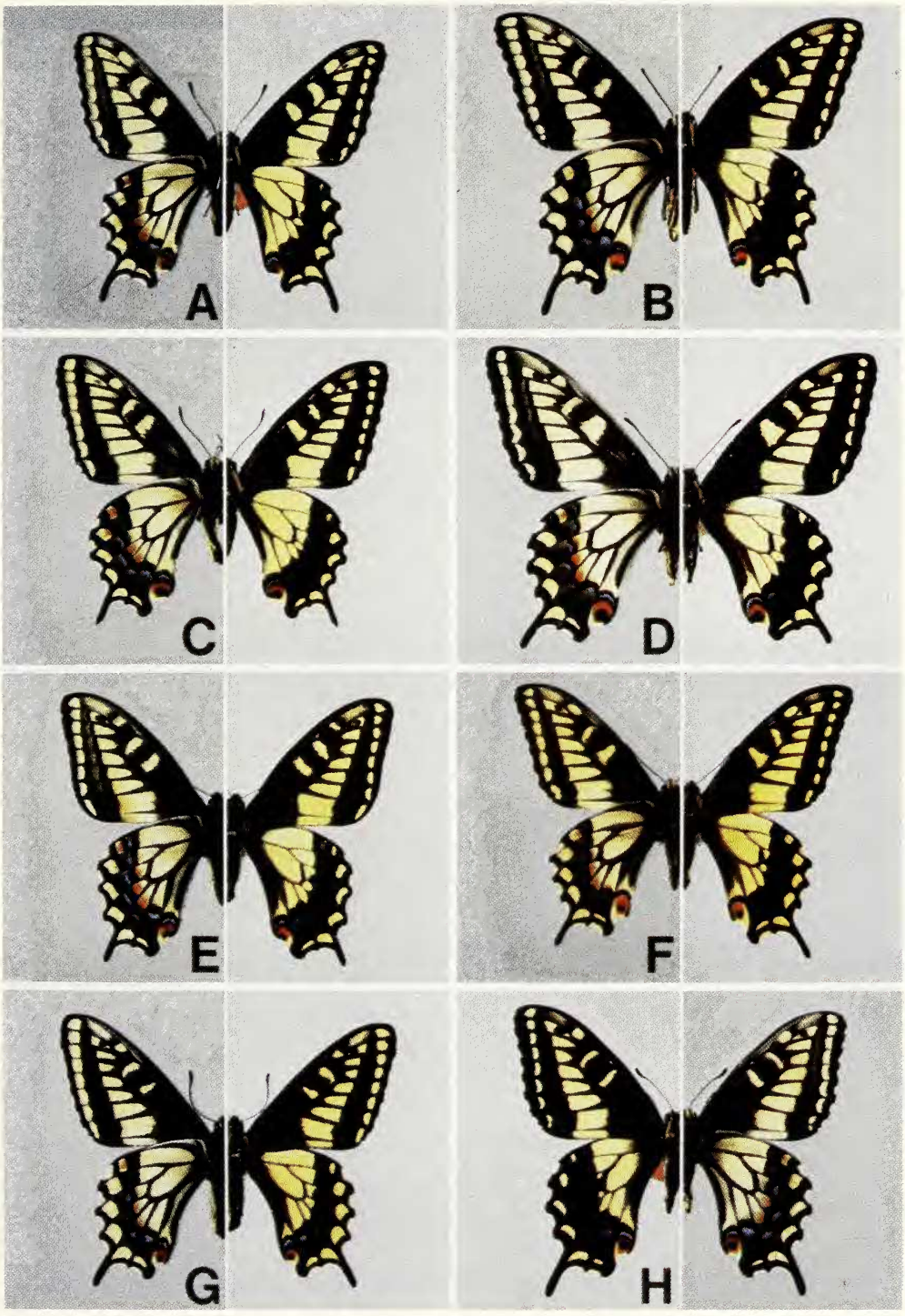
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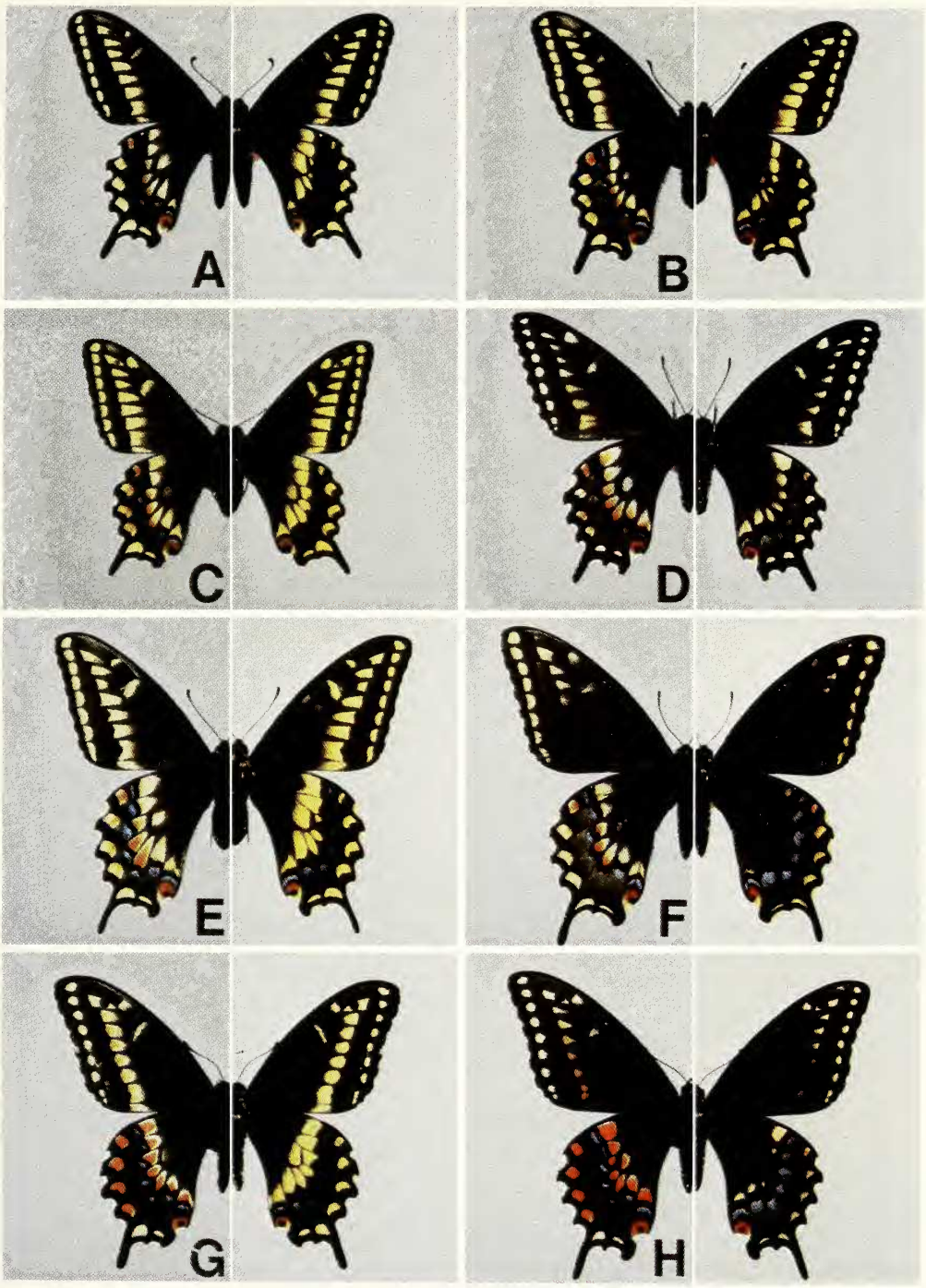
Plate 3. Color pattern of dark morphs of *P. machaon* group species. Each specimen has dorsal and ventral views of right wings figured on right and left sides, respectively: a, *P. zelicaon*, male Wintering Hills, 18 km S of Drumheller, Alberta, May 30, 1982; b, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, *Ex* larva, coll. 15 July -7 Aug. 1982, on *Zizia aptera*; c, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, June 23, 1974; d, *P. polyxenes* X *machaon*, female Duck Mountain Park, Manitoba, *Ex* larva, coll. 25 June 1980, on *Zizia aptera*; e, *P. m. bairdii*, male Sunset Crater, E of Flagstaff, Arizona, May 5, 1980; f, *P. m. bairdii*, female Flagstaff, Arizona, May 27, 1980; g, *P. p. asterius*, male Burlington, Ontario, *Ex* larva, coll. Aug. 1981, on garden carrot; h, *P. p. asterius*, female Burlington, Ontario, *Ex* larva, coll. Aug. 1981, on garden carrot.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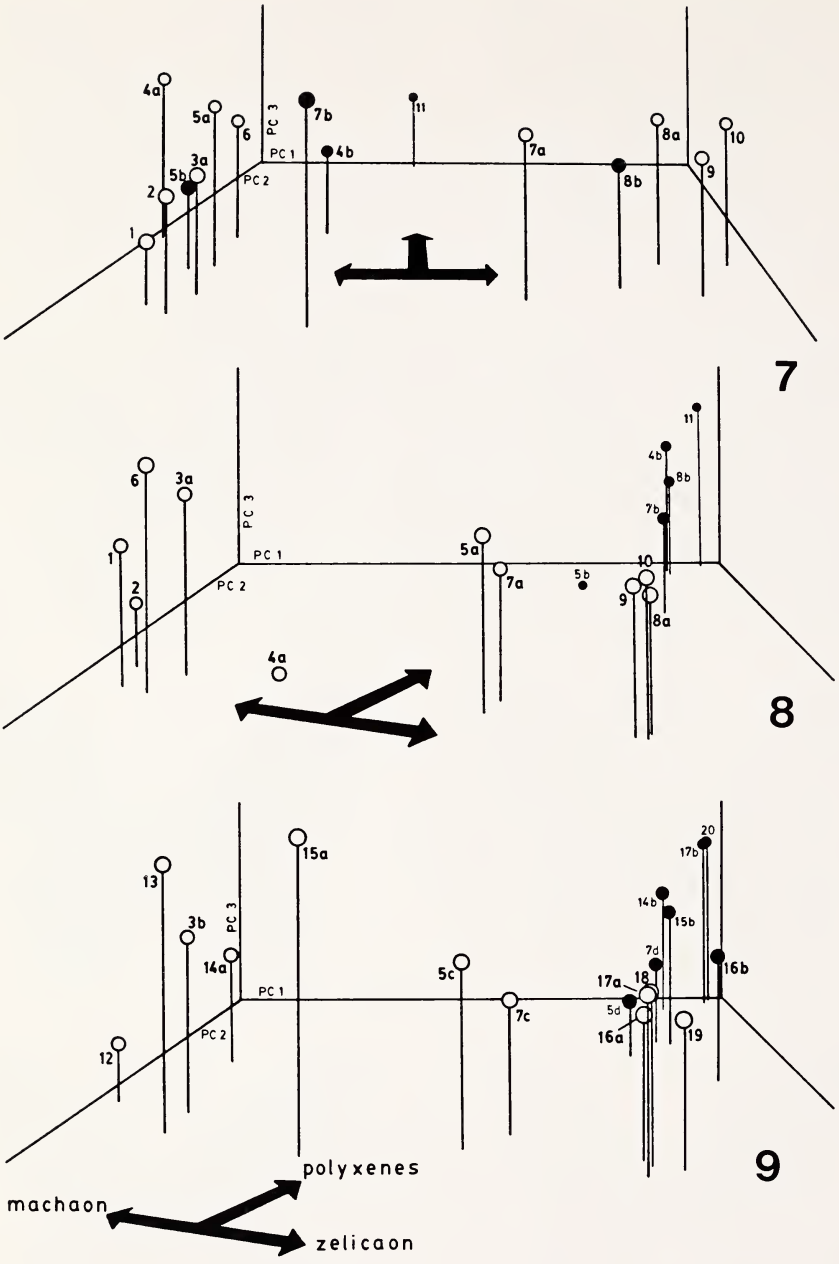
G
H



Figures 7 to 9. Mean scores of representative populations plotted on first three principal component axes. See Table 4 for key to locations. Black circles indicate black morph adults, and empty circles indicate yellow morph adults. PC 1, PC 2 and PC 3 refer to the first, second and third principal component axes. Figure 7. 3D.PCA on electrophoretic data alone Populations include only individuals used in the original analysis. Figure 8. 3D.PCA on morphometric data alone Populations include only individuals used in the original analysis. Figure 9. Additional samples scored with morphometric loadings. Populations are partly or completely composed of individuals not included in original analysis, but scored with factor loadings from PCA on morphometric data alone. Most populations are either topotypic or from close to type localities.

Table 4. Population samples of the *P. machaon* species group used in Figures 7–9.

Letter after taxon name indicates yellow color morph (Y) or black color morph (B).

No. in figs.	Locality and region	Sample size	Taxon and color morph
1.	Clayhurst Fy., Peace R. area, British Columbia	20	*P. m. pikei*
2.	Pink Mt., northern British Columbia	36	*P. m. aliaska*
3a.	Thompson, northern Manitoba	37	*P. m. hudsonianus*
3b.	Thompson, northern Manitoba	46	*P. m. hudsonianus* (expanded sample)
4a.	Duck Mt. Park, central Manitoba	1	*P. machaon X polyxenes* -Y
4b.	Duck Mt. Park, central Manitoba	7	*P. polyxenes X machaon* -B
5a.	Drumheller, southern Alberta	79	*P. m. dodi* -Y
5b.	Drumheller, southern Alberta	2	*P. m. dodi* -B
5c.	Drumheller, southern Alberta	105	*P. m. dodi* -Y (expanded sample)
5d.	Drumheller, southern Alberta	3	*P. m. dodi* -B (expanded sample)
6.	Kamloops, southern British Columbia	48	*P. m. oregonius*
7a.	Bragg Creek, south-central Alberta	65	*P. zelicaon X machaon* -Y
7b.	Bragg Creek, south-central Alberta	7	*P. zelicaon X machaon* -B
7c.	Bragg Creek, south-central Alberta	160	*P. zelicaon X machaon* -Y (expanded sample)
7d.	Bragg Creek, south-central Alberta	44	*P. zelicaon X machaon* -B (expanded sample)
8a.	Wintering Hills - West, southern Alberta	17	*P. zelicaon* -Y
8b.	Wintering Hills - West, southern Alberta	3	*P. zelicaon* -B
9.	Thunder Mt., northern British Columbia	23	*P. zelicaon*
10.	Vancouver area, southern British Columbia	10	*P. zelicaon*
11.	Caledonia, southern Wisconsin	15	*P. p. asterius*
12.	Steese Hwy., central Alaska	39	*P. m. aliaska*
13.	The Dalles area, northern Oregon	8	*P. m. oregonius*
14a.	Riding Mt. Park, central Manitoba	33	*P. m. hudsonianus* and *P. polyxenes X machaon* -Y
14b.	Riding Mt. Park, central Manitoba	32	*P. p. asterius* and *P. polyxenes X machaon* -B
15a.	Salida Co., southern Colorado	9	*P. m. bairdii*-Y
15b.	Salida Co., southern Colorado	17	*P. m. bairdii*-B
16a.	Judith Mts., central Montana	10	*P. zelicaon* -Y
16b.	Judith Mts., central Montana	8	*P. zelicaon* -B

(continued on next page)

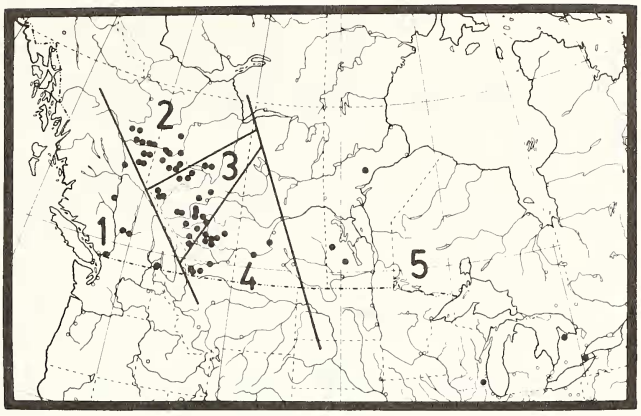
Table 4 (continued)

No. in figs.	Locality and region	Sample size	Taxon and color morph
17a.	Jefferson Co., northern Colorado	19	*P. zelicaon* -Y
17b.	Jefferson Co., northern Colorado	24	*P. p. asterius* -B
18.	Gothic, central Colorado	25	*P. zelicaon* -Y
19.	San Francisco area, central California	27	*P. zelicaon*
20.	Ottawa to Point Pelee, Ontario	59	*P. p. asterius*

to *P. machaon* from other regions, especially in electrophoretic characters. Specimens from prairie hilltops were more likely to belong to *P. zelicaon*. This situation was well illustrated by the locality samples from the Drumheller region. The sample from the river bank just above the town of Drumheller contained only *P. m. dodi* and a few intermediate specimens. There were mostly *P. zelicaon* in the samples from the Hand Hills and the western part of the Wintering Hills, which are about 15 and 12 km, respectively, from the nearest deeply cut river valleys or ravines. A mixture of both species was at a hilltop on the eastern part of the Wintering Hills, about 4 km from the nearest deep ravine and 6 km from the banks of the Red Deer River.

This pattern was basically the same as that in southern British Columbia, where *P. m. oregonius* lives in the dry grassland habitats of the central Interior, while *P. zelicaon* is far more common in forested and wetter habitats. In the Peace River region *P. m. pikei* also tended to occur on the dry river banks and *P. zelicaon* on the hills farther away from the river. However, an added complication is that another subspecies, *P. m. aliaska*, frequents the boreal and especially the alpine regions of northern British Columbia, north of the Peace River.

In the predominantly forested regions of central Alberta, there seemed to be a different sort of relationship between *P. machaon* and *P. zelicaon* (Figure 11 and 14). At the northern localities (Marten Mt. to Adams Lkt.) there was a predominance of electrophoretic and morphometric character combinations which tended to resemble *P. zelicaon*, as well as a significant proportion of more intermediate individuals. However, a few individuals were indistinguishable from northern *P. machaon* even with the two character types considered together, and it was unclear whether these formed a distinctive group from the others. In the more southerly localities (Buck Lk. to Bragg Cr.), the different phenotypes evident in the north tended to merge even more. Populations from single localities were composed of a few individuals indistinguishable from either *P. machaon* or *P. zelicaon*, but the majority was intermediate. There was a single peak near the midpoint between the two extremes, which tapered off to either side. The different phenotypes all occurred within the same habitat as well. Though electrophoretic and morphometric characters showed a generally concordant pattern, electrophoretic character combinations were more obviously intermediate than were morphometric characters.



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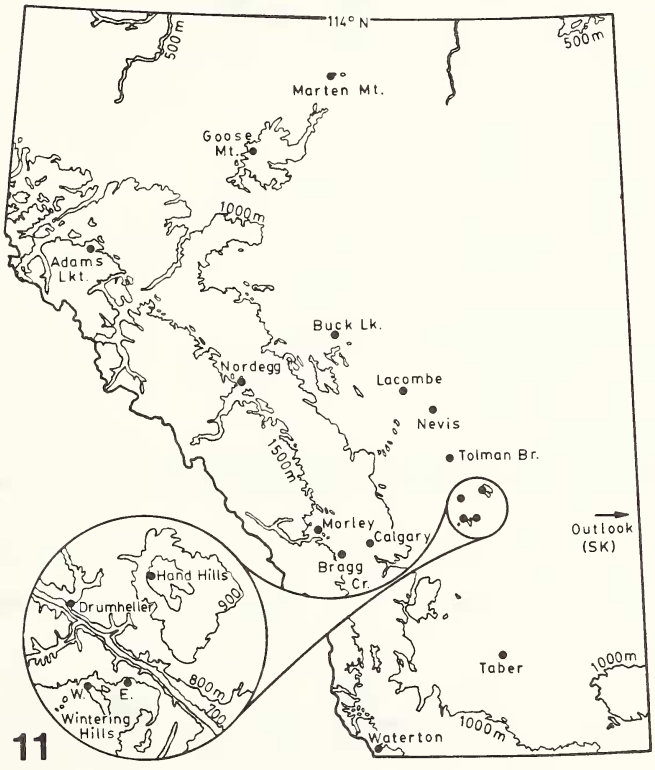

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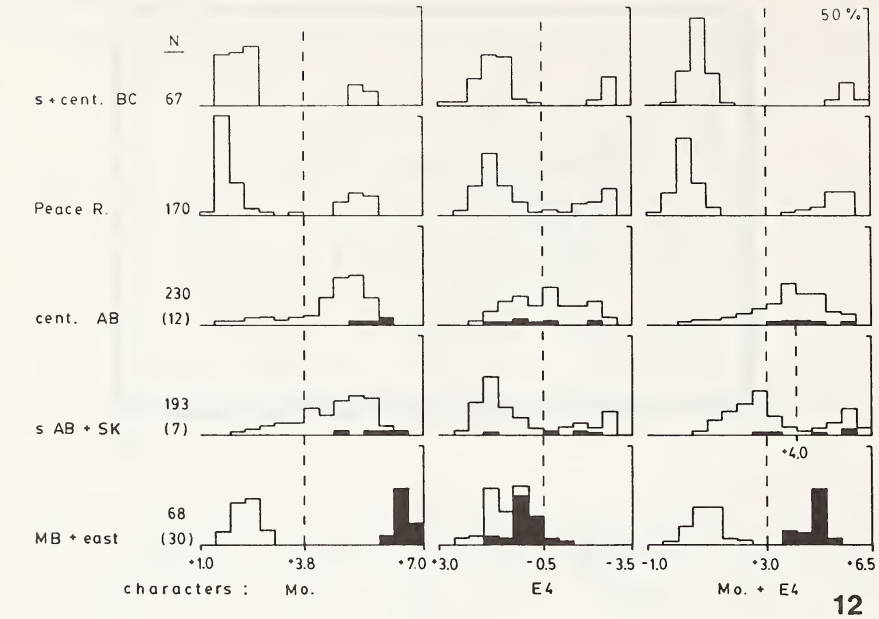
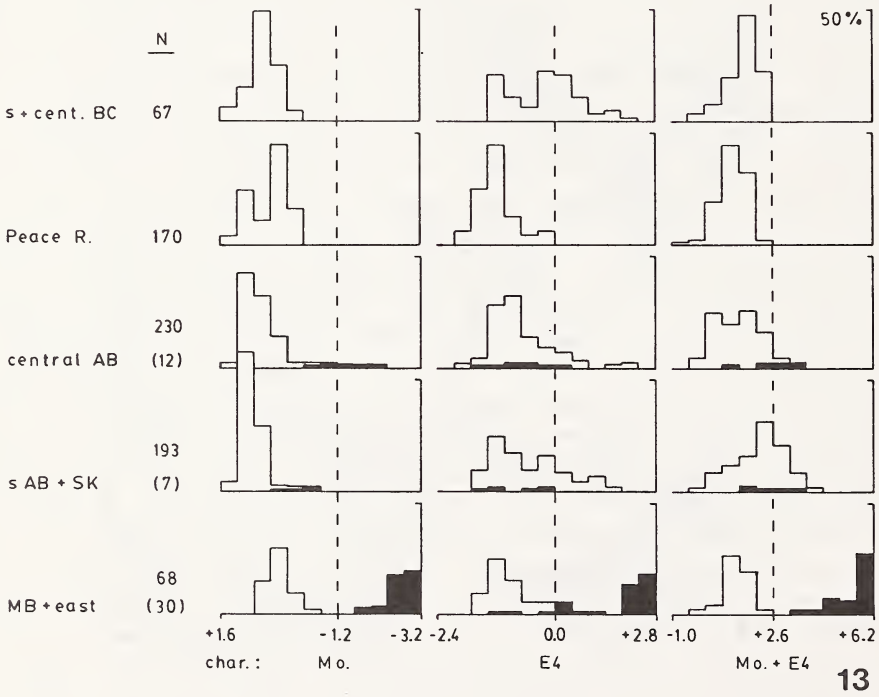
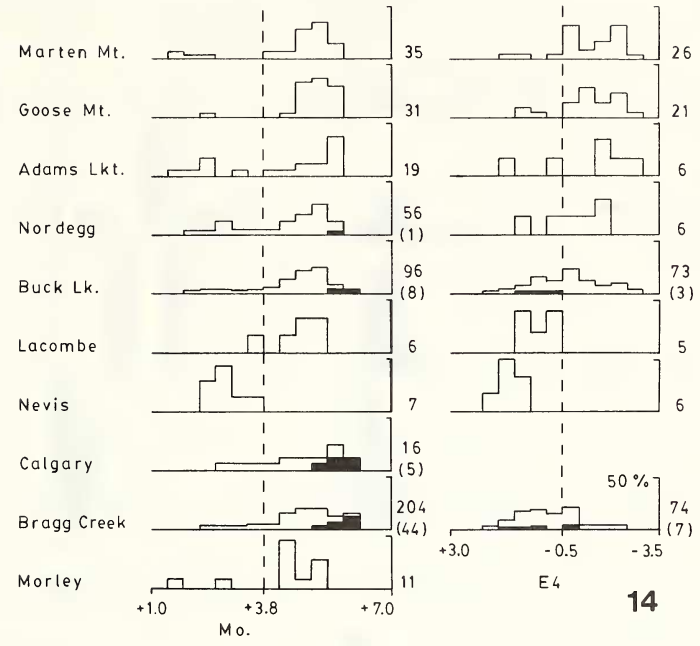
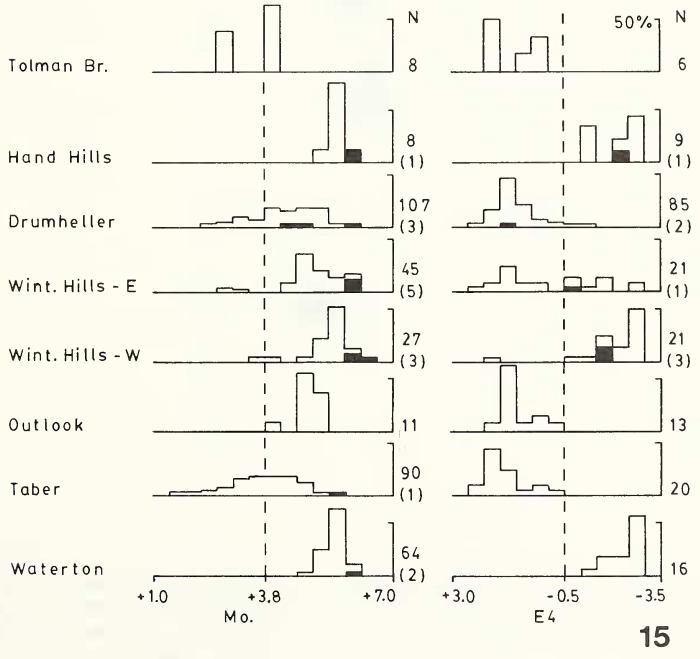
Figures 10 and 11. Figure 10. Western Canada, showing 5 major regions: 1, southern and central British Columbia (s+cent. BC); 2, Peace River region (Peace R.); 3, central Alberta (cent. AB); 4, southern Alberta and Saskatchewan (s AB+SK); 5, Manitoba and eastward (MB+east). Dots show localities from which specimens were used in the initial PCAs. Figure 11. Central and southern Alberta, with major localities. Localities refer to those used in figures 14 and 15.



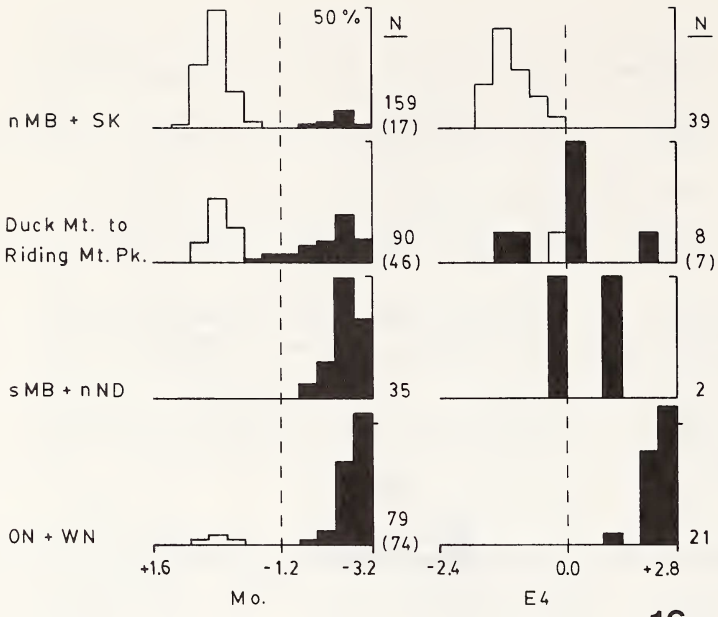


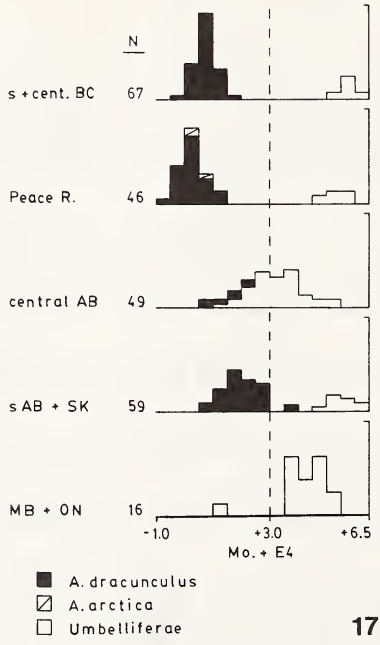
Figures 12 and 13. Component axes of three separate PCAs, with frequency histograms of all individuals in each of five major geographic regions (see Figure 10). Only specimens used in original PCAs are included. Darkened portions of histograms indicate black morphs. Dashed lines indicate divisions between taxa. Mo. = morphometic characters. E4 = electrophoretic characters. Figure 12. First component axes, by major region Figure 13. Second component axes, by major region



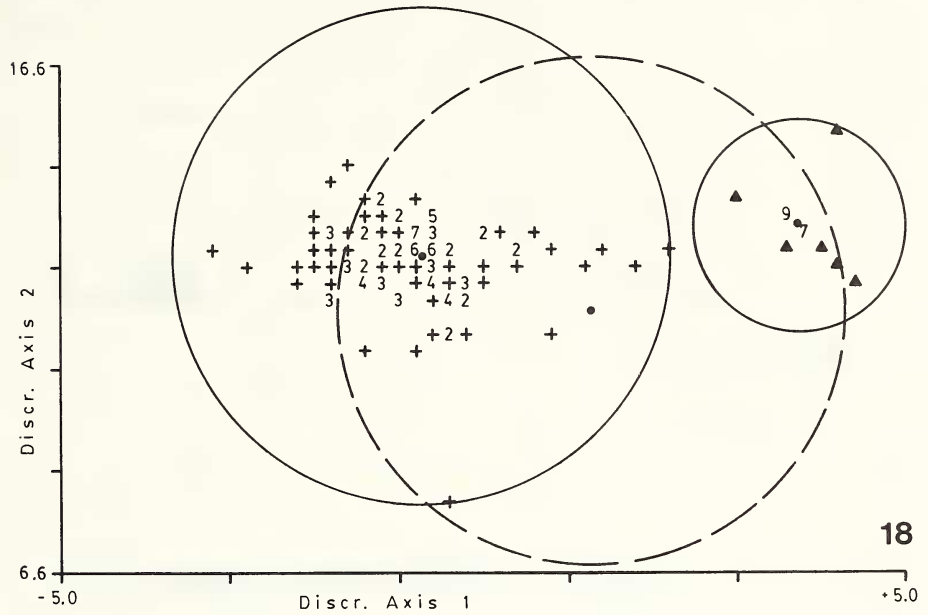


Figures 14 and 15. Locality samples plotted on first component axes. Some samples include individuals not used in original PCAs. Darkened parts of histograms indicate black morphs. Dashed lines indicate divisions between taxa. Mo. = morphometric characters. E4 = electrophoretic characters. Figure 14. Central Alberta samples plotted on PC.1. Figure 15. Southern Alberta and Saskatchewan samples on PC.1.

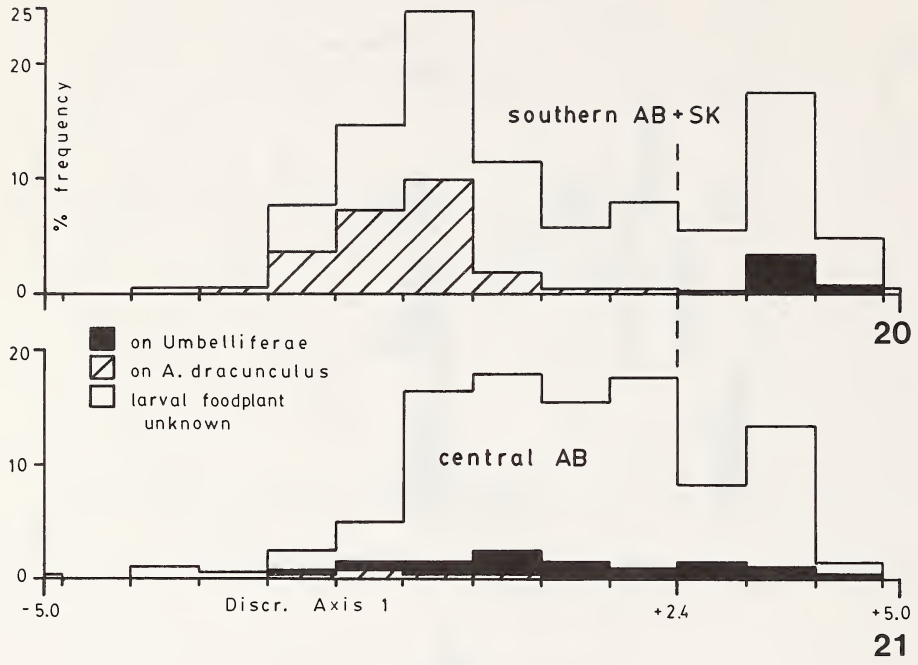




Figures 16 and 17. Dashed lines indicate divisions between taxa. Mo.= morphometric characters. E4 = electrophoretic characters. Figure 16. Area samples from Manitoba and eastward. Samples are plotted on second component axes, and some include individuals not included in original PCAs. Black morph individuals are indicated by darkened portions of histograms. Geographic areas: n MB + SK = northern Manitoba and northern Saskatchewan; Duck Mt. to Riding Mt. Pk. = Duck Mountain and Riding Mountain Parks; s MB + n ND = southern Manitoba and northern North Dakota; ON + WN = Ontario and Wisconsin. Figure 17. Adults reared from wild-collected larvae Histogram key: darkened = larvae on *Artemisia dracunculus*; cross-hatched = on *Artemisia arctica*, clear = on umbelliferous larval hostplants. Individuals are plotted on first component axis of PCA on combined character set and include only those used in original PCA. Regions refer to those indicated in Figure 10.



Figures 18 and 19. Reared adults plotted on discriminant axes, including only those used in original discriminant analyses. Numbers indicate more than one data point with the same coordinates. Circles indicate maximum diameters of the three original groups. Dashed lines indicate locations of populations from opposite figure. Figure 18. 2D.DFA plot of reared samples: southern Alberta. On *A. dracunculus* (+) N=119; on umbellifers (triangles) N=22. Figure 19. 2D.DFA plot of reared samples: central Alberta. Only umbellifer-reared individuals shown, N=45.



Figures 20 and 21. All adults from central and southern Alberta (AB), and southern Saskatchewan (SK), plotted on first discriminant axis. Reared individuals are indicated as subsets. Figure 20. All southern Alberta and Saskatchewan specimens, plotted on DFA.1 N=497, including N=119 reared from *A. dracunculus* and N=22 reared from umbellifers.

Figure 21. All central Alberta specimens, plotted on DFA.1 N=481, including N=7 reared from *A. dracunculus* and N=45 reared from umbellifers.

The most *P. machaon*-like individuals from the southern foothills of Alberta had morphometric character combinations more similar to *P. m. hudsonianus* than to *P. m. dodi*. In fact, no specimens were collected on the southern prairies which were as *P. m. hudsonianus* or *P. m. aliaska*-like as a few individuals taken at Bragg Creek and Buck Lake, localities geographically close to *P. m. dodi* populations. This suggests that the hybrid populations are at least partly a product of hybridization between *P. zelicaon* and the more northerly *P. machaon* races, rather than with *P. m. dodi*. On the other hand, most of the specimens from these two localities tended to be very similar to *P. m. dodi* in morphometric characters, while most were more intermediate between *P. zelicaon* and *P. machaon* in electrophoretic characters. This suggests that the very similar wing and body color pattern combinations which occur in both *P. m. dodi* and the hybrid swarms may have arisen in different ways.

In Alberta, the morph with black wings occurred together with the more common yellow members of both *P. machaon* and *P. zelicaon*. The former specimens had a range of electrophoretic character combinations matching the remainder of the population with which they occurred. This applied to individuals collected with other *P. zelicaon* specimens on prairie hilltops, the intermediate hybrid populations of the Alberta foothills, and the *P. m. dodi* collected along dry river banks. On this basis it appears as though this morph has become a

regular part of all of these populations. Although the color pattern of the black morph in many respects resembles that of *P. p. asterius*, there was no good electrophoretic evidence of hybridization with *P. polyxenes* in these populations.

The situation in Manitoba was far less clear (Figure 16), though there probably are hybrid swarm populations in this region as well. These hybrid populations appear to be the result of interactions between *P. machaon* and *P. polyxenes*, rather than between *P. machaon* and *P. zelicaon* as in central Alberta. The dramatic effect of the gene for the black wing morph made it more difficult to demonstrate phenotypic intermediacy in morphometric characters, and I was able to subject only a small number of individuals from central Manitoba to electrophoretic analysis. However, populations scored on the second PC axis tended to be intermediate in electrophoretic characters. Also a sizable proportion of black morph individuals in central Manitoba tended to take on character states found in *P. machaon*. For example, most had a club-shaped anal pupil and many had more yellow on the tegulae and apical forewing cell than in *P. p. asterius* from southern Ontario or the United States.

Adult characters versus larval foodplants.— Separation of *P. machaon* from *P. zelicaon* and *P. polyxenes* on the basis of electrophoretic and morphometric characters was supported by a comparison of larval foodplants. Scores of adults reared from larvae collected on *Artemisia* were plotted against those of individuals from various species of Umbelliferae, on the first PC axis derived from both the electrophoretic and the morphometric characters combined (Figure 17). In the Peace River region, individuals reared on *Artemisia arctica* from alpine habitats grouped with those reared on *Artemisia dracunculus* from dry, grassy river banks. The *P. machaon* from southern Alberta and Saskatchewan, reared on *A. dracunculus*, were also separated from *P. zelicaon* on this basis, although their more similar morphometric characters resulted in a somewhat closer grouping. The single *P. machaon*-like individual reared from central Manitoba was obtained on an umbellifer.

The specimens reared on *A. dracunculus* from central Alberta were collected at Nevis Junction, on a northward extension of prairie habitat along the Red Deer River. These adults resembled those of *P. m. dodi* from further south along the river and were undoubtedly just an outlying population of this race. They also, however, resembled some specimens collected on umbellifers farther to the west. Larvae of the hybrid populations from central Alberta feed on umbellifers, and in this respect are similar to *P. zelicaon*. Reared material showed the same wide range of phenotypes as the wild- collected adults.

Since PCAs on the total sample from western Canada provided only a partial separation between *P. machaon* and *P. zelicaon* from central and southern Alberta on the basis of morphometric characters, I attempted to improve the separation with discriminant factor analysis (DFA) of foodplant groups. Three foodplant groups were defined. The first included all specimens reared from *A. dracunculus* in either southern or central Alberta. The second included all material from umbellifers in the southern Alberta region, all of which were from *Angelica*, *Lomatium* or *Heracleum* in the Waterton Park and Crowsnest Pass area. The third group included all the adults reared from umbellifers in the central Alberta region. The morphometric characters used in this analysis were the same as those used in the PCAs, except that only 10 characters were used because one character (tegula color) showed no variation in the groups defined above. The discriminant axis loadings are included in Table 12.

As with the PCAs on electrophoretic characters, the DFA gave a fairly good separation of *P. machaon* and *P. zelicaon* in southern Alberta (Figures 18–19). However, the umbellifer feeders from central Alberta did not separate very well from either of the other two groups. With all

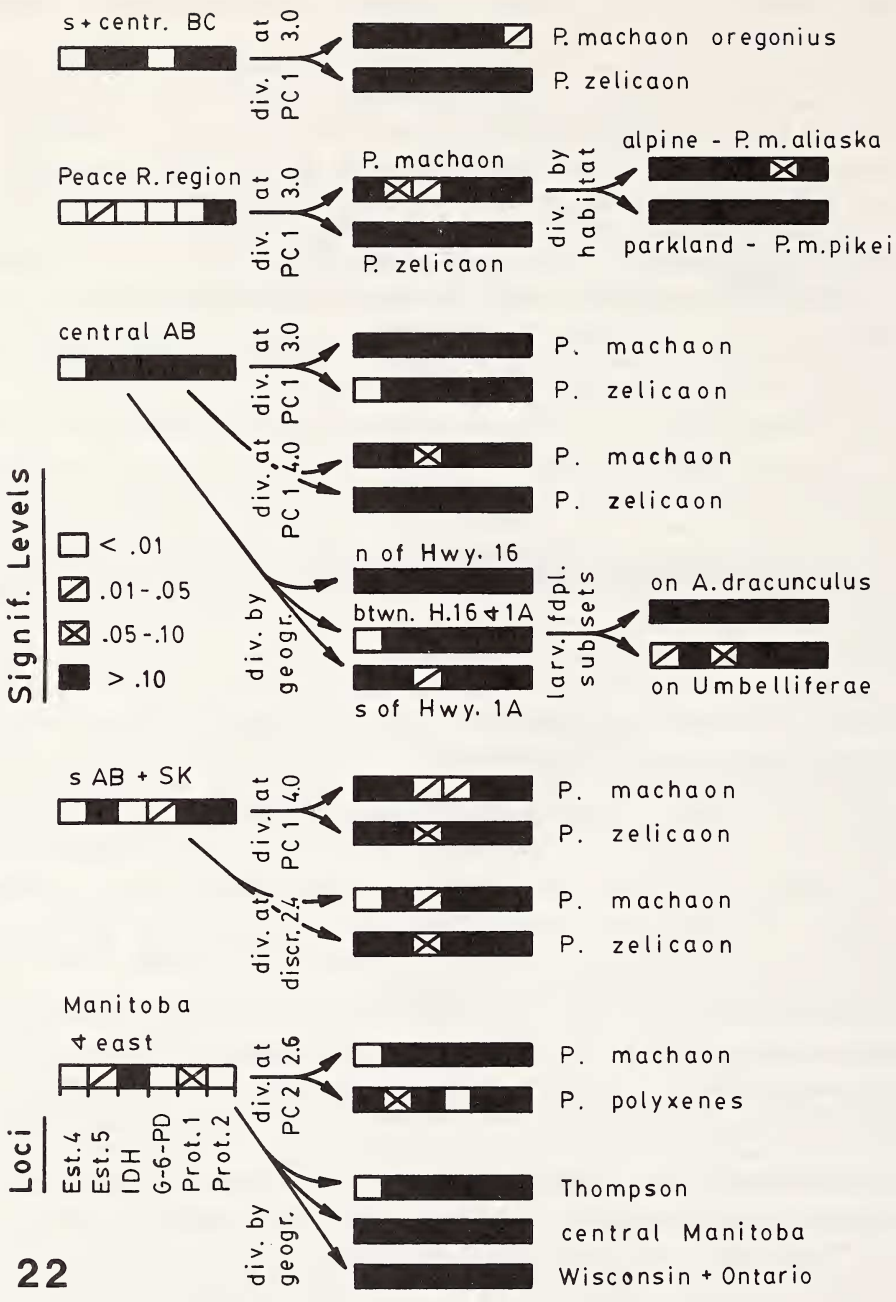


Figure 22. Hardy-Weinberg equilibrium tests on subpopulations. Six loci are shown as squares within bar for each population. Significance levels (key at center left) refer to deviation from equilibrium. Names for some populations refer to population divisions based on artificial criteria, such as arbitrary points on discriminant axes.

wild collected adults from these regions scored on the first discriminant axis (Figures 20–21), a distribution appeared of character combinations similar to that obtained from reared material. This indicated that the reared material probably included a representative sample of the foodplants which larvae of these populations feed on in nature.

Tests for Hardy-Weinberg equilibrium.— Chi-squared tests for deviation from Hardy-Weinberg (HW) proportions of enzyme genotypes were used as an indication of whether or not gene flow occured relatively freely within populations. A sample showing a significant excess of homozygous genotypes at a particular locus then suggests some sort of behavioral or genetic incompatibility between the different alleles. In this study, I assume that homozygous excesses indicate likelihood of positive assortative mating or higher heterozygote mortalities, which in turn suggest the presence of more than one species. I also assume that the different enzyme banding patterns are inherited, and for that reason I refer to "loci" rather than "electrophoretic characters" in this section.

Figure 22 includes all six loci which showed a difference from HW proportions at the 5% level in at least one of the five major geographic regions. Since numerous tests for HW equlibrium were performed, at least some of these are likely to show spurious differences.

HW tests on the six loci showed that all five of the major regions had at least one locus with proportions of genotypes different from equilibrium at the 1% level. This suggested more than one species in each region. However, the pattern of deviation from equilibrium and the loci that deviated were different in each of the region.

In southern and central British Columbia, highly significant excesses were identified of homozygous genotypes at the Est4 and G-6-PD loci. These excesses disappeared when the total regional sample was divided into two groups on the basis of the clusters formed on the first PC axis of the analysis on both electrophoretic and morphometric characters, and the tests were rerun. This corroborates the hypothesis that two species are in that region. The *P. m. oregonius* subsample showed an excess of heterozygotes of the Prot2 locus which was significant at the 3.3 % level. No biological explanation is offered for this.

The total sample from the Peace River region showed large deviations from equilibrium in five of the six loci, due to homozygote excesses. When it was subdivided in the same way as for southern British Columbia, most of these excesses were eliminated in the *P. machaon* and *P. zelicaon* subsamples. A further subdivision of *P. machaon* on the basis of habitat eliminated the slight excesses in the Est5 and IDH loci, and supported the division of *P. machaon* in this region into two ecological races, *P. m. aliaska* and *P. m. pikei*. However, a small homozygote excess showed up in *P. m. aliaska* in the Prot1 locus. The biological significance of this, if any, is unknown, though a reasonably large allele frequency difference at this locus between the two races should be noted.

The central Alberta regional sample was very different from the previous two, despite the fact that the total sample had fairly high frequencies of both of the pairs of alleles at the Est4 and G-6-PD loci which normally distinguish *P. machaon* and *P. zelicaon*. The total sample contained genotypes not much different from equilibrium at any of the loci, except Est4. When *P. machaon* was separated from *P. zelicaon* in the same way as for the Peace River and southern British Columbia regions, the highly significant homozygote excess was retained in the *P. zelicaon* zelicaon subsample. A division of the total sample at 4.0, rather than 3.0, on the same PCA axis showed a slightly significant excess of heterozygotes at the IDH locus. Clearly, the second division furnished subsamples more consistent with the hypothesis that there are two species in that region. However, it divided the total central Alberta sample down the middle of

Table 5. Morphometric character state distributions for population samples of the *P. machaon* species group

Abbreviations: n of H.16 = central Alberta region, north of Highway 16, Hwy. 16-1A = central Alberta region between Highways 16 and 1A, s+c BC = southern and central British Columbia, s AB = southern Alberta. DHW = dorsal hindwing, VFW = ventral forewing.

Character	State	*Papilio machaon* *oregonius*	*aliaska*	*pikei*	*hudsonianus*	*dodi*	*Papilio zelicaon* X *machaon* n of H.16	Hwy. 16-1A	Bragg Cr.	*Papilio zelicaon* s+c BC	Peace area	s AB	*Papilio polyxenes asterias*	*Papilio polyxenes* X *machaon*
	N:	55	41	79	37	147	62	90	72	12	50	52	21	10
1. DHW anal yellow	1	5.5	92.7	49.4	94.6	23.1	72.6	72.2	72.2	75.0	74.0	84.6	100.0	90.0
	2	27.3	7.3	34.2	5.4	51.7	24.2	24.4	23.6	16.7	22.0	11.5		10.0
	3	56.4		16.6		25.2	3.2	3.3	4.2	8.3	4.0	3.8		
	4	10.9												
2. DHW pupil shape	1	7.3	87.8	43.0	10.8	2.7	3.2	1.1						
	2	83.6	12.2	51.9	86.6	81.0	14.5	41.1	68.1	8.3	2.0		4.8	80.0
	3	9.1		5.1	2.7	14.3	32.3	31.1	27.8		20.0	5.8	61.9	20.0
	4					2.0	50.0	26.7	4.2	91.7	78.0	94.2	33.3	
3. DHW blue/red sep.	1	36.4	82.9	77.2	32.4	2.7	8.1	7.8	5.6					10.0
	2	32.7	17.1	19.0	29.7	17.7	11.3	25.6	29.2		8.0	1.9		20.0
	3	30.9		3.8	37.8	79.6	80.6	66.7	65.3	100.0	92.0	98.1	100.0	70.0
4. tegula color	1	100.0	100.0	100.0	100.0	99.3	100.0	98.9	98.6	100.0	100.0	100.0		30.0
	2					0.7		1.1	1.4				19.0	40.0
	3												81.0	30.0
5. VFW discal color	1	100.0	92.7	100.0	89.2	10.2	11.3	4.4	11.1		2.0			
	2		7.3		8.1	22.4	16.1	15.6	11.1		10.0			
	3					29.3	24.2	33.3	19.4	16.7	28.0	5.8		10.0
	4				2.7	38.1	48.4	46.7	58.3	83.3	60.0	94.2	100.0	90.0
6. VFW apical smudge	1	100.0	100.0	100.0	100.0	100.0	100.0	96.7	93.1	100.0	100.0	96.2		20.0
	2							3.3	6.9			3.8	33.3	30.0
	3												66.7	50.0

Table 5. continued

Character	State	*Papilio machaon* *oregonius*	*aliaska*	*pikei*	*hudsonianus*	*dodi*	*Papilio zelicaon* X *machaon* n of H.16	Hwy. 16-1A	Bragg Cr.	*Papilio zelicaon* s+c BC	Peace area	s AB	*Papilio polyxenes asterias*	*Papilio polyxenes* X *machaon*
7. VHW postmedian orange	1-2	12.8	34.1	70.9	45.9	5.4	8.0	7.7	4.2	8.3	8.0	1.9		
	3-4	80.0	65.9	29.1	54.1	88.2	80.6	77.8	72.2	91.7	82.0	80.4		10.0
	5-6	7.2				2.0	9.7	3.3	11.1		8.0	7.7		20.0
	7-8					4.0	1.6	11.2	12.5		2.0		100.0	70.0
8. metathoracic color	1	100.0	100.0	100.0	100.0	27.2	11.3	12.2	20.8		4.0			10.0
	2					71.4	88.7	76.7	58.3	100.0	96.0	82.7		
	3					1.4		11.1	20.8			17.3	100.0	90.0
9. abd. ventral line	1-3	98.2	100.0	100.0	100.0	21.8	12.9	10.0	16.7		4.0			
	4-5	1.8				6.1	87.1	4.4	4.2					10.0
	6-7					9.5		2.2	5.6			1.9		
	8-9					62.2		81.1	73.6	100.0	96.0	98.1	100.0	90.0
10. abd. lateral line	1	100.0	100.0	100.0	100.0	98.6	100.0	93.3	90.3	100.0	100.0	90.4		10.0
	2					1.4		1.1	1.4			1.9		
	3							5.6	8.3			7.7	100.0	90.0
11. abd. upper line	1-3								4.2					90.0
	4-5				16.2			6.7	9.7			1.9		
	6-7		14.7	2.5	45.9	3.4	3.2	13.3	23.6			3.8		
	8-9	100.0	85.3	97.5	37.8	96.6	96.8	80.0	62.5	100.0	100.0	94.2	100.0	10.0

Table 6. Allele frequencies, by region, taxon and hybrid assemblage of the *P. machaon* species group.

Abbreviations: see caption for Table 5.

			Papilio machaon					*Papilio machaon* X *zelicaon*			*Papilio zelicaon*			*Papilio polyxenes asterias*	*Papilio polyxenes* X *machaon*
			oregonius		*pikei*		*dodi*	n of	Hwy 16	Bragg	cent.				
				aliaska		*hudsonianus*		Hwy 16	to 1A	Creek	+ s	Peace			
Locus	Allele	RF				(Thompson)					BC	region	s AB	WN + ON	cent. MB
αGPD		(n)	57	50	92	39	170	76	102	79	12	61	60	21	10
	A	.29											0.017		
	B	.32	0.974	1.000	1.000	1.000	1.000	0.993	1.000	0.994	1.000	1.000	0.975	1.000	1.000
	C	.35	0.026					0.007		0.006			0.008		
G-6-PD		(n)	55	50	90	39	157	66	96	74	12	61	56	21	10
	E	.16										0.008			
	A	.18		0.020	0.128	0.038	0.006	0.136	0.047	0.027		0.016			0.200
	B	.20	0.073	0.010	0.039	0.026	0.089	0.455	0.370	0.385	0.958	0.762	0.759		0.050
	I	.22	0.064		0.011		0.092								0.050
	K	.24			0.006		0.003	0.030	0.026	0.007		0.016	0.008	0.976	
	C	.26	0.800	0.970	0.817	0.936	0.739	0.311	0.510	0.554	0.042	0.172	0.214	0.024	0.700
	D	.30	0.064				0.070	0.038	0.042	0.027		0.025	0.018		
IDH		(n)	55	50	85	39	154	63	96	74	12	61	56	21	10
	A	.16	0.091			0.026	0.045	0.008	0.057	0.007					
	B	.18	0.664	0.720	0.947	0.679	0.545	0.873	0.724	0.689	1.000	0.984	0.938	1.000	0.900
	C	.20	0.045	0.020		0.026	0.049	0.008	0.026	0.027			0.036		
	D	.22	0.182	0.260	0.053	0.269	0.360	0.111	0.193	0.277		0.016	0.027		0.100
	E	.24	0.018												
MDH		(n)	57	50	93	39	165	70	102	74	12	63	17	21	10
	I	.16									0.042		0.018		
	A	.18		0.030	0.005	0.038	0.006	0.021	0.054	0.047			0.009		
	B	.22	1.000	0.970	0.995	0.962	0.988	0.979	0.946	0.946	0.958	1.000	0.964	0.976	0.950
	C	.26					0.006			0.007			0.009	0.024	0.050
ME		(n)	55	50	91	39	162	71	96	79	12	61	56	21	10
	J	.475	0.009											0.071	
	I	.500	0.164	0.010		0.077	0.046	0.021	0.010	0.038	0.083			0.071	0.100
	A	.525	0.291	0.170	0.242	0.244	0.185	0.056	0.047	0.051	0.125	0.074	0.027	0.143	0.100
	B	.550	0.536	0.820	0.758	0.641	0.707	0.908	0.901	0.880	0.792	0.893	0.857	0.643	0.750
	K	.575					0.006	0.014	0.010				0.027		0.050
	C	.600				0.038	0.052		0.031	0.032		0.033	0.089	0.048	
	D	.625					0.003							0.024	

Table 6. continued

Locus	Allele RF		*Papilio machaon* *oregonius*	*aliaska*	*pikei*	*hudsonianus* (Thompson)	*dodi*	*Papilio machaon* X *zelicaon* n of Hwy 16	Hwy 16 to 1A	Bragg Creek	*Papilio zelicaon* cent. + s BC	Peace region	s AB	*Papilio polyxenes asterias* WN + ON	*Papilio polyxenes* X *machaon* cent. MB
ODH		(n)	55	48	84	39	156	63	96	74	12	59	56	21	10
A	.17		0.009	0.021		0.115	0.006	0.040	0.063	0.162		0.102	0.036		0.050
B	.21		0.991	0.760	0.958	0.795	0.994	0.857	0.875	0.811	1.000	0.822	0.946	1.000	0.950
C	.25			0.219	0.042	0.090		0.103	0.063	0.027		0.076	0.018		
APK		(n)	55	45	82	39	154	63	96	74	12	53	56	21	10
A	.55		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.991	1.000	1.000
B	.60												0.009		
Est4		(n)	59	50	98	39	163	75	102	79	12	61	59	21	10
A	.48		1.000	0.920	0.954	0.897	0.954	0.293	0.475	0.677		0.074	0.085	1.000	0.950
B	.54			0.080	0.046	0.103	0.046	0.707	0.525	0.323	1.000	0.925	0.915		0.050
Est5		(n)	59	50	96	39	163	75	102	79	12	61	56	21	10
I	.57		0.008				0.009			0.006					
A	.64		0.297	0.080	0.510	0.077	0.337	0.053	0.108	0.146		0.049	0.071		0.150
B	.65				0.010	0.013		0.007				0.008			0.050
C	.71		0.695	0.920	0.479	0.910	0.653	0.893	0.873	0.842	0.958	0.902	0.929	0.952	0.800
D	.75							0.047	0.020	0.006	0.042	0.041		0.048	
Prot1		(n)	55	45	82	39	154	63	96	74	12	52	56	21	10
A	.21		1.000	0.789	0.598	0.897	0.997	0.976	0.969	0.926	1.000	0.952	1.000	1.000	1.000
B	.26			0.211	0.402	0.103	0.003	0.278	0.060	0.375		0.048			
Prot2		(n)	55	45	82	39	154	63	96	74	12	52	56	21	10
I	.300					0.064	0.026		0.010	0.007		0.019			
A	.315		0.400	0.022	0.018	0.038	0.224	0.071	0.130	0.088	0.333	0.135	0.455	0.500	0.976
B	.330		0.600	0.956	0.970	0.897	0.727	0.921	0.844	0.905	0.667	0.837	0.536	0.500	0.024
C	.345			0.022	0.012		0.023	0.008	0.016			0.010	0.009		
Heterozygosity:			0.233	0.155	0.188	0.203	0.218	0.196	0.219	0.246	0.076	0.162	0.158	0.078	0.191

a somewhat bell-shaped curve of character combinations (Figure 12), and may simply reflect the large contribution of the Est4 locus to the scores on that axis.

With division of the sample from central Alberta region into three subregions (a northern, middle and southern one), both the northern and southern subregions appeared not to be significantly different from equilibrium at the Est4 locus either, despite the higher proportion of alleles characteristic of *P. zelicaon* in the northern subregion (Table 6). This was especially interesting in the sample for the southern subregion, since it was composed of specimens from only a single locality at Bragg Creek. The deviation from equilibrium in the Bragg Creek sample at the IDH locus was caused by an excess of heterozygotes. The sample from the middle subregion continued to show an excess of homozygotes at Est4. With specimens reared on different foodplants considered separately, it was clear that a slightly less significant excess remained at that locus. These adults were obtained from larvae collected on *Heracleum* plants (Umbelliferae).

The highly significant homozygote excess was retained even with the largest sample from a single locality in that subregion, Buck Lake, considered separately (not shown on Figure 22). This locality is, to my knowledge, about 80 km from the nearest stand of *Artemisia dracunculus*. These results suggest that *P. machaon* and *P. zelicaon* have merged their gene pools in a large part of the central Alberta region, although not all loci are at equilibrium in the middle part of that region.

The regional sample from southern Alberta and Saskatchewan showed significant homozygote excesses at three loci. A division of the sample on the basis of scores on the first PCA axis of the analysis on both morphometric and electrophoretic characters eliminated the excess at the Est4 locus, but only reduced it at the IDH and G-6-PD loci. With the sample divided on the basis of scores on the first axis of the discriminant analysis of reared specimens, the homozygote excesses were retained at the Est4 and IDH loci. Division of the sample from this region into two species is supported by the fact that the homozygote excesses were partially reduced even when the sample was subdivided on the basis of just morphometric characters.

However, this subdivision is not as good as that effected in the southern British Columbia and Peace River regions. One reason may be a higher probability of incorrect species assignment, because of the greater morphometric similarity between *P. machaon* and *P. zelicaon* from this region. A second explanation is that, even though the species retain a separate genetic identity, there is a biologically significant amount of gene introgression between the species. The rate of introgression may differ between loci, as for example between Est4 and G-6-PD. This suggestion is supported by the fact that these two loci have very similar differences in allele frequency between *P. machaon* and *P. zelicaon* in the southern British Columbia and Peace River regions, and yet G-6-PD seems to have reached equilibrium before Est4 in the middle part of the hybrid zone in central Alberta.

In the region that included samples from Manitoba, Wisconsin and Ontario, there was also evidence for two species, with some hybridization between them. Here the main alleles distinguishing between *P. polyxenes* and *P. machaon* were G-6-PD and Prot2, rather than G-6-PD and Est4, as between *P. zelicaon* and *P. machaon*. The total regional sample had several significant deviations from equilibrium. When it was divided on the basis of scores on the second PCA axis using both morphometric and electrophoretic characters, which essentially separated black morph from yellow morph individuals, then a highly significant deviation remained at the G-6-PD locus in the sample comprised of black morph specimens. These deviations were eliminated when the region was divided geographically into three subregions.

The main difference from the previous subdivision was that one yellow morph and nine black morph specimens were placed in a group by themselves. Under both schemes there was a significant excess of homozygotes in the Est4 locus of the northern Manitoba sample, because of presence at Thompson of two individuals homozygous for the "B" allele (most common in *P. zelicaon*), compared with only four heterozygous individuals and 33 individuals homozygous for the "A" allele (most common in *P. machaon* and *P. polyxenes*). I can offer no convincing biological explanation for this situation, since Thompson is many hundreds of kilometers from the nearest localities where *P. zelicaon* specimens have been found. Instead, I suspect, it may be due to sampling error. Clearly, more work is needed to ascertain species relationships in Manitoba.

Diagnosis of Adults and Ranking of Taxa

To tabulate character variation quantitatively, 13 major populations were defined. The arrangement of these groups was based on both electrophoretic and morphometric characters, and the groups resemble those described in the previous sections involving multivariate analyses and Hardy-Weinberg equilibria. Table 6, for electrophoretic characters, includes some specimens for which not all loci were scored, but for which it was possible to be certain of their identification by reference to their morphometric characters. Table 5, for morphometric characters, includes data only for those specimens used in the PCAs.

Papilio machaon.— In general, *P. machaon* adults from western Canada were distinguished by yellow hair on the ventral part of the thorax and abdomen, yellow scales covering most of the forewing disc on the ventral side, and the anal pupil connected to the wing margin, whether club shaped or a thin line. This result verifies the utility of the color pattern characters of adults used by others to identify this species (*e.g.,* Edwards, 1883; Dornfeld, 1980). In electrophoretic characters, *P. machaon* individuals were distinguished by the A allele at Est4, the C allele at G-6-PD and a relatively high proportion of D alleles at IDH.

P. m. dodi specimens were more difficult to identify in the absence of electrophoretic information, but could best be distinguished from the *P. zelicaon* populations sympatric with them by the club shaped, connected anal pupil. I have examined the types of *P. m. dodi* in the Canadian National Collection, and they definitely belong to the race of *P. machaon* whose larvae feed on *Artemisia dracunculus* on the prairies of southern Alberta and Saskatchewan.

Subspecies of *P. machaon* in western Canada were best separated from each other by locality and habitat, though there were major changes in the frequency of particular states of several characters, including IDH, ODH, Est4, Prot1 and Prot2. Though almost all specimens of *P. m. oregonius* and *P. m. dodi* from western Canada are distinguished by both adult and larval color pattern, these two subspecies grade into each other in western Montana and southern Idaho. Since the zone of intergradation is narrow, relative to the phenetically more homogeneous ranges of the subspecies, I recognize the populations on either side of the continental divide in Montana and northward as separate subspecies.

I am uncertain of the extent and location of the intergradation between these subspecies south of Montana. In Utah and Colorado, the black adult wing morph becomes more common (Emmel, 1975) and the name *P. machaon bairdii* should be applied. The name *P. brucei* has been applied to yellow morph adults in polymorphic populations within the range of *P. m. bairdii*(Figure 42). Its type locality is from the northern part of the major clinal shift to yellow forms, and its use in a subspecific sense is probably not of much value. I follow the practice of Fisher (1980) and Miller and Brown (1981) in treating the name as a junior synomym of *P. m.*

bairdii.

The previous subdivision of the southern subspecies of *P. machaon* as separate species is probably a consequence of W.H. Edwards' relatively typological species concept, and the natural tendency of many workers to view the black morph adults as fundamentally different from the yellow morph adults. However, black morph adults of *P. machaon* occur in low frequencies as far north as Drumheller, Alberta, where they are electrophoretically identical to the yellow morph adults. Hence, I feel that the inclusion of *P. bairdii* in *P. machaon* is an inescapable consequence of the application of the biological species concept to geographic clines. Fisher (1980) has also recognised the specific unity of all the *Artemisia dracunculus*-feeding populations in the western United States.

Papilio zelicaon and hybrids.— Most *P. zelicaon* individuals from western Canada are recognized by the black hair on the ventral part of the thorax and abdomen, black or almost black ventral forewing disc and the rounded, centered anal pupil. As in *P. machaon*, these characters match those previously used in traditional taxonomic treatments. Important diagnostic electrophoretic characters included the B allele in both the Est4 and G-6-PD loci.

I do not believe that formal subspecific divisions are justified in *P. zelicaon*. The species is composed of innumerable slightly differentiated populations with adult features that grade into each other. Local foodplant and climatic adaptations of most populations are usually far more pronounced than are the relatively minor differences in morphometric characteristics. I believe that the recent practice, of referring to the populations that Remington (1968a) named *P. gothica* as *P. zelicaon nitra*, is unwarranted. Yellow morph adults are more common than the black form even at the type locality of *P. nitra*, and I find the eastern and western yellow morphs of *P. zelicaon* to be impossible to separate with any degree of consistency.

The presumed type of *P. zelicaon* Lucas was examined for me in considerable detail by G.E. Ball in 1980, on a trip he made to the Paris Museum. Using Ball's description and comparative material, as well as photographs of the specimen (taken by J.J. Menier), features of *P. zelicaon* were checked against Remington's (1968a) diagnosis of *P. gothica*. The specimen is closer to Remington's conception of *P. gothica* than his conception of *P. zelicaon*. This is not surprising, since as Shapiro (1975) and Emmel and Shields (1980) pointed out, *P. zelicaon* from the type locality in central California has undergone basic ecological changes since its description in 1852, while the remaining populations at higher altitudes in central California are still very similar in appearance to topotypic *P. gothica*.

In some regions, particularly central Alberta, a high proportion of individuals exhibited intermediate character states, or character combinations which placed them in an intermediate position between *P. zelicaon* and *P. machaon*. These were considered to be hybrids (individuals of mixed ancestry), and such individuals formed the majority of some populations. Since these populations included individuals with phenotypes occupying the complete range between the typical parental forms, many individuals were difficult to identify as hybrids. Hybrid populations were also highly variable in composition, and were only identified as such when they showed a unimodal distribution of phenotypes, of which the peak was clearly intermediate between the parental species.

The *P. zelicaon X machaon* hybrid swarms in the Cypress Hills have been much less completely documented than those in central Alberta. I designate these populations as hybrid swarms mainly because most individuals look very similar to the hybrid material collected in the southern part of central Alberta. As well, they are intermediate in wing and body pattern between the *P. machaon* and *P. zelicaon* specimens collected in the prairie habitats surrounding

the Cypress Hills.

In regions where hybridization between *P. zelicaon* and *P. machaon* is rare, possibly there are structural isolating mechanisms between the species, in addition to behavioral ones. This was suggested by the only natural interspecific mating which I have observed in such regions of sympatry. The mating took place at Taylor, at a site where *P. m. pikei* adults are common, and involved a fresh *P. zelicaon* female and slightly worn *P. machaon* male. They remained in copula for at least 11 hours before they separated. Such an abnormally long mating (Clarke and , 1956b) may result from disturbance of being netted, but seems more likely to be due to some sort of prezygotic mating disfunction.

Papilio polyxenes and hybrids.— Most specimens of *P. polyxenes* were easily distinguished from those of *P. zelicaon*, *P. machaon* and their hybrids by the much greater amount of black scales on the hindwing, covering more than half of the hindwing disc, and yellow spots rather than a broad yellow band on the sides of the abdomen. Separation was also based on the K allele of G-6-PD and the A allele of Prot2.

A small proportion of *P. polyxenes*-like individuals were noted in *P. zelicaon*, *P. machaon* and their hybrids in western Canada. These, however, had the same electrophoretic alleles as the yellow morph individuals with which they were found, and were also distinguished from *P. polyxenes* by the greater amount of yellow on the tegula and apex of the forewing, as well as the lesser amount of orange on the postmedian band of the ventral hindwing. The black morph specimens of *P. zelicaon* from Alberta prairies were identical in appearance to a series which I have seen from the type locality of *P. nitra* in Montana, and so there is no reason to expect these individuals to comprise a separate species outside of western Canada.

Although the morphometric differences between *P. zelicaon* and *P. polyxenes* in western Canada suggest a greater ease of species identification than Fisher (1980) reported in Colorado, I expect that I would have found similar difficulties if I had been able to obtain a larger sample from localities where these two species are in closer contact in southern Saskatchewan.

Since the interactions of *P. polyxenes* with *P. machaon* and *P. zelicaon* in western Canada are not well understood, I rely on the opinions of authors who are familiar with the three species in the western United States (*e.g.,* Ferris and Emmel, 1982; Fisher, 1977 and 1980), and who have consistently reported that *P. polyxenes* maintains a distinct genetic identity from both *P. zelicaon* and *P. machaon* throughout most of their region of potential interaction. As well, although electrophoretic characters indicate some intermediacy in central Manitoba, samples of *P. polyxenes* from Ontario and Wisconsin are as different from *P. zelicaon* and *P. machaon* as these two species are from each other.

Most of the specimens of *P. polyxenes* from southern Manitoba are indistinguishable in appearance from *P. p. asterius* from Ontario and the eastern United States. The remainder show signs of introgression with *P. machaon*. Specimens exhibiting substantial introgression are designated as *P. polyxenes X machaon* hybrids. The identification of such natural hybrid specimens is supported by comparisons with those obtained by artificial hybridization. In particular, many of the adults collected in central Manitoba appear very similar or identical to the hybrids obtained by other workers (see particularly Clarke and , 1953, 1955a; Ae, 1961, 1964; Remington, 1958, 1968a). The same applies to hybrid specimens of *P. zelicaon* and *P. machaon* from central Alberta. These studies clearly indicate the genetic basis of these characters, and for this reason I have used several of these characters in the morphometric portion of this study. I consider the similarity between the experimentally produced and

wild-collected specimens to be adequate evidence for the hybrid origin of the collected material.

Two taxonomic descriptions refer to adult forms which are due to hybridization between *P. polyxenes* and *P. machaon*. These are *P. kahli* and *P. m. avinoffi*, both of which are referred to in this study either as black or yellow wing morph adults of *P. polyxenes X machaon*, or as *P. polyxenes X machaon* and *P. machaon X polyxenes*, respectively. My use of these names is based on photographs I have seen of the holotypes. I have also seen several paratypes, but these differ slightly from one another, as well as from the holotype. At least one of the female paratypes of *P. kahli* in the Canadian National Collection seems to me to be identical to typical *P. p. asterius* specimens. My opinion was apparently shared by J.D. McDunnough, who indicated his opinion on a folded slip of paper attached to the specimen pin.

Specimens which fit the description of *P. m. avinoffi* were obtained by Remington (1958, 1968a), when he crossed two comparatively yellowish individuals of the black adult morph from central Manitoba, and got some yellow morph as well as black morph offspring. The *avinoffi* form tends to grade into more typical *P. m. hudsonianus* and so identification of specimens is arbitrary.

The systematic relationship of *P. polyxenes* and *P. machaon* in central Manitoba clearly needs more investigation than I have provided in the present study. The recognition of central Manitoba populations as interspecific hybrid populations, rather than as intermediates between subspecies, allows the retention of established taxonomic practice, pending a more thorough study of these two taxa in this region, as well as elsewhere in their ranges.

Ranking and accuracy of identification.— The distribution of morphometric and electrophoretic character states showed, in several ways, that more than one species of the *P. machaon* group was present in western Canada. First, multivariate analysis of either of these two character suites indicated three major clusters of individuals in western Canada, and two major clusters in each of four of the five regions in western Canada. Second, the proportions of enzyme genotypes suggested interruptions to gene flow which corresponded to the breaks between clusters in most of western Canada. Third, the morphometric and electrophoretic character distributions showed good correspondence with each other, as well as with ecological features such as preferred habitat and larval foodplant. This character concordance applied to areas where there appeared to be a large amount of interspecific hybridization, as well as those in which species appeared to interbreed very little. The characters of wing and body color pattern, which had been used by taxonomists in the past to distinguish among species, proved useful under critical examination. A few electrophoretic loci were also diagnostic for species, and so gave additional information about inter- and intra-population relationships.

However, evidence of hybridization between each of the three species showed that recognition of some populations as species, and others as interspecific hybrid swarms or subspecies, was partially arbitrary. This was resolved by an arrangement reflecting the fact that species hybridize only rarely over most of their sympatric range, and that also involved a minimum of change in existing taxonomic arrangements. Since previous taxonomic arrangements were not based on electrophoretic characters, consideration of these allowed an independent test of the biological significance of these arrangements.

The electrophoretic characters also allowed a more direct comparison with the degree of genetic similarity between species of other, unrelated, taxa. This comparison was obtained by calculating Nei's (1972) Genetic Identity (*I*) for all combinations of each of the 13 geographically separated populations of the *P. machaon* group which showed little or no internal interruption in gene flow. Nei's Genetic Identity is the most commonly used of several

Table 7. Nei (1972) Genetic Identity and Distance for taxa and hybrid assemblages of the *P. machaon* species group.

Mean Genetic Identity is below diagonal and mean Genetic Distance is above diagonal.

	Population	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1.	*P.m. oregonius*	*****	0.043	0.053	0.029	0.010	0.124	0.072	0.054	0.226	0.196	0.179	0.017	0.145
2.	*P.m. aliaska*	0.958	*****	0.038	0.006	0.032	0.094	0.052	0.032	0.234	0.170	0.192	0.047	0.233
3.	*P.m. pikei*	0.948	0.963	*****	0.045	0.046	0.123	0.086	0.063	0.258	0.195	0.219	0.062	0.249
4.	*P.m. hudsonianus*	0.972	0.994	0.956	*****	0.022	0.191	0.049	0.029	0.221	0.165	0.181	0.038	0.217
5.	*P.m. dodi*	0.990	0.969	0.955	0.978	*****	0.102	0.053	0.034	0.217	0.176	0.172	0.027	0.177
6.	*P.m.X z.*:n of H.16	0.884	0.911	0.884	0.913	0.903	*****	0.010	0.028	0.039	0.014	0.031	0.097	0.232
7.	*P.m.X z.*:Hwy 1A-16	0.930	0.949	0.918	0.953	0.949	0.990	*****	0.007	0.069	0.039	0.048	0.058	0.202
8.	*P.m.X z.*:Bragg Cr.	0.947	0.968	0.939	0.971	0.967	0.972	0.993	*****	0.108	0.069	0.083	0.048	0.204
9.	*P.zelicaon* : s. BC	0.797	0.791	0.773	0.802	0.805	0.962	0.933	0.898	*****	0.011	0.008	0.188	0.267
10.	*P.zelicaon* : Peace	0.822	0.843	0.823	0.848	0.838	0.986	0.961	0.933	0.989	*****	0.013	0.161	0.276
11.	*P.zelicaon* : s. AB	0.836	0.826	0.803	0.835	0.842	0.970	0.953	0.920	0.992	0.987	*****	0.140	0.219
12.	*P.m. X p.*: c. MB	0.984	0.954	0.940	0.962	0.974	0.908	0.943	0.953	0.829	0.851	0.870	*****	0.109
13.	*P. polyxenes*	0.865	0.792	0.780	0.805	0.838	0.793	0.817	0.815	0.766	0.758	0.803	0.897	*****

standardized genetic similarity coefficients, and *I* has been determined for a wide variety of taxa.

Of the 13 major populations distinguished in this study, all pairs listed as separate species had *I* values less than or close to 0.85 (Table 7). These pairs included those populations from the three regions in which *P. machaon* and *P. zelicaon* occur sympatrically. Thorpe (1982) showed that when two populations have an *I* value of less than 0.85, the probability is very high that they are distinct species. Thus, despite difficulties in separating individuals of some populations on the basis of morphometric characters, as well as the presence of several hybrid swarms, genetic similarity coefficients based on elctrophoretic characters suggest that at least the main clusters were different enough to rank as separate species.

I values can also be used to make intraspecific pairwise comparisons. About 80% of conspecific I values are above 0.95 (Thorpe, 1982). In the present study, all comparisons of populations within *P. machaon* and *P. zelicaon* were close to or above 0.95.

The interval between 0.85 and 0.95 is occupied by a few values from interspecific pairs and a much larger proportion of intraspecific pairs. In the *P. machaon* group, those comparisons involving hybrid swarms and one of the parental species generally show *I* values between 0.85 and 0.95. Several of these, however, resemble one parental species more than the other and show *I* values above 0.95 when compared with the more similar species. For example, the northern part of the *P. machaon X zelicaon* swarm is closer to *P. zelicaon* while the southern part (Bragg Creek) is more similar to *P. machaon.* This result could have been expected on the basis of morphometric character similarities. However, the central Manitoba population is much more like *P. machaon* than *P. polyxenes*, a result in contrast to that which might be expected on the basis of morphometric similarities (for rough comparisons see 3D.PCA scores in Figures 7–9).

Without information about locality, habitat or electrophoretic alleles, I estimate that I am able to correctly identify 95% of all specimens from western Canada as members of one of the groups listed in the key in the previous chapter. My accuracy is probably higher for distinguishing *P. machaon* from *P. zelicaon* in the absence of a large hybrid swarm. *P. zelicaon X machaon* and *P. polyxenes X machaon* hybrids, as well as *P. m. dodi*, are more difficult to distinguish from each other and I estimate that I can correctly identify about three quarters of all such specimens with only morphometric information.

Diagnosis of specimens on the basis of morphometric characters in the key was found to be fairly reliable when compared to scores obtained from PCA factor loadings. Several characters used in the keys were not used in the original multivariate character analyses, generally because they were difficult to score consistently. Both the key and PCA factors produce arbitrary divisions which are not particularly meaningful in hybrid populations.

Since the five subspecies of *P. machaon* are allopatric, or parapatric and separated by habitat in western Canada (see next section), it is possible to obtain a more precise estimate of accuracy of identification. Using habitat and geographic range to define groups, I performed a discriminant function analysis on the five subspecies, using the morphometric and electrophoretic characters which were employed in the multivariate analyses in previous sections. Since sample sizes were small, only the 27 variables which showed more than 10% variation in frequency between groups were used. The results are contained in Table 8.

This analysis indicates that a high frequency of correct identification can be achieved for these taxa if both major character suites are used. The lowest accuracy, 76% for *P. m. hudsonianus*, is still fairly high. If only the 11 morphometric characters listed in Table 2 are

Table 8. Frequency of correct identification of subspecies of *Papilio machaon*.

Values based on discriminant function analysis (DFA) of 27 morphometric and electrophoretic characters. Classification percent shows frequency of correct identification (*e.g.*, 82.9% for *P. m. aliaska*) and incorrect identification (*e.g.*, 9.8 and 7.2 % of *P. m. aliaska* were misclassified as *P. m. hudsonianus* and *P. m. pikei*, respectively).

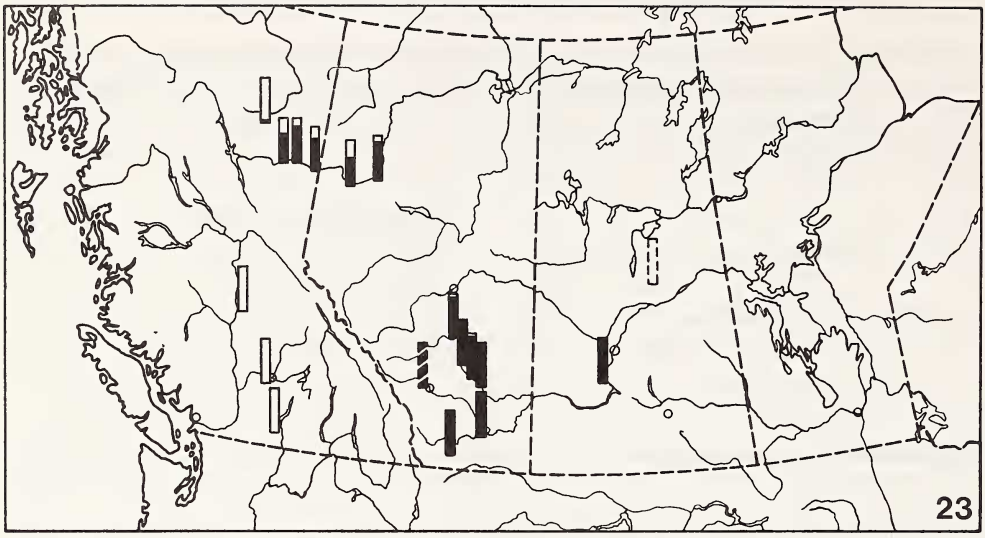
			% Classification with DFA				
	Defined Groups	N	1.	2.	3.	4.	5.
1.	*P. m. aliaska*	41	82.9	9.8	7.3		
2.	*P. m. hudsonianus*	37	16.2	75.7	8.1		
3.	*P. m. pikei*	79	7.6	1.3	88.6	2.5	
4.	*P. m. oregonius*	55	1.8		1.8	96.4	
5.	*P. m. dodi*	147			1.4	7.5	91.2

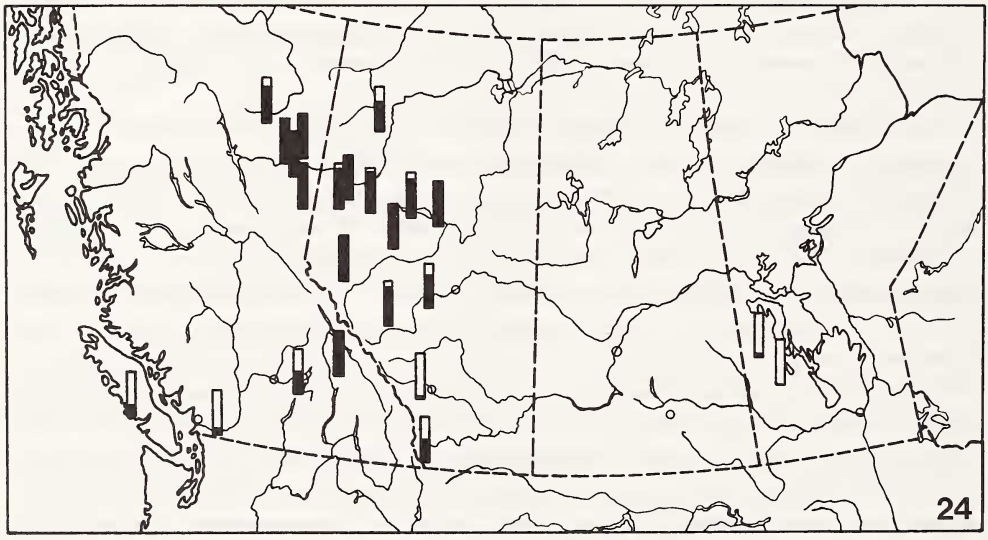
used in a new DFA, rather than the 27 morphometric and electrophoretic characters used to obtain the results in Table 9, then the lowest accuracy is 62%, again for *P. m. hudsonianus*. However, if forewing length and tail length are added to these 11 characters, and a third DFA is performed, then the accuracy of correct identification of *P. m. hudsonianus* rises to 70%, and the lowest is 68%, for *P. m. pikei*. I estimate that my personal lowest accuracy of identification of these five *P. machaon* subspecies is 75% if characters such as wing shape and color are considered, which are difficult to quantify for computer work.

It is difficult to obtain a precise assessment of the relative systematic utility of morphometric and electrophoretic characters in the context of the present study. The morphometric characters were chosen on the basis of their variability within western Canada, and also as a means of comparison to systematic descriptions and diagnoses. Electrophoretic characters were selected much more randomly, since any protein that showed consistent, simple banding patterns was used. As well, only three loci showed more than 50% allele frequency differences between populations, and it is possible that results were affected by sampling error. Furthermore, the coding scheme for morphometric characters was somewhat different from that used for electrophoretic characters in the principal components analyses. A more strictly analogous scheme would have reduced the number of electrophoretic characters from 42 to 10, a number more comparable to the 11 morphometric characters used. Despite these factors, it is clear that electrophoretic analysis is of considerable systematic utility (*cf* Wake, 1981). The large degree of correspondence of the two types of characters in the context of the present study is a demonstration of the potential usefulness of electrophoretic analysis in systematic research on species complexes.

Larval Color Pattern

Larvae of *P. machaon*, *P. zelicaon* and *P. polyxenes* do not show consistent interspecific differences in color pattern, though intraspecific variability is marked. Most fifth instar larvae of these three species are predominantly green, with a prominent black band extending around each segment, and six colored spots on most segments. Within populations, the background green color varies from pale bluish-green to bright emerald green, and the black bands vary considerably in width. Color of the segmental spots varies from lemon yellow to orange-red.





Figures 23 and 24. Frequencies of spot color in larvae of the *P. machaon* group in western Canada. Dark areas of histograms indicate orange or red spots, and light areas indicate yellow spots. Figure 23. Spot colors of larvae collected on composites. Histograms with broken borders indicate small sample sizes. Figure 24. Spot colors of larvae collected on umbellifers.

CORRIGENDA–*Quaestiones Entomologicae*, Volume 22(4)

Griffiths, G.C.D. (1986, 22: 253–260).–Relative Abundance of the Root Maggots *Delia radicum* (L.) and *D. floralis* (Fallén) (Diptera: Anthomyiidae) as Pests of Canola in Alberta.

page

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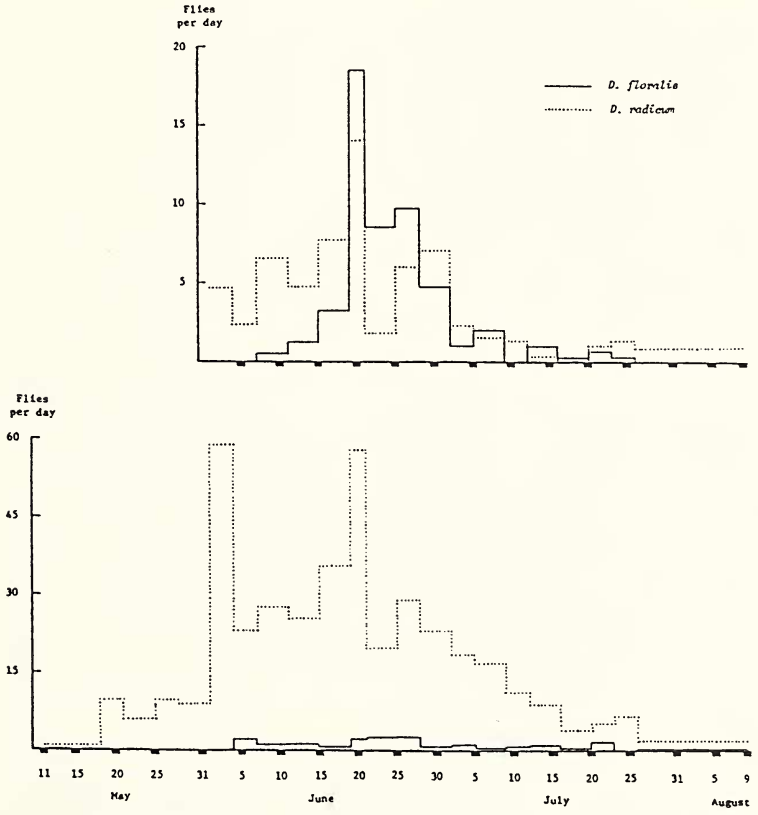
Fig. 2

Substitute following figure for the one on page 256.



The larvae of *P. alexanor* have a color pattern which is very similar to that of the above three species, despite a very different adult wing pattern. *P. indra* and *P. hospiton* each have a larval color pattern which is divergent from that of the other species in the *P. machaon* group, but which is more similar to that of other *P. machaon* group members than to other *Papilio*.

Color of the segmental spots on mature larvae is consistent on individuals, but many larval populations are composed of discrete color classes with few intermediates. Clarke and Knudsen (1953) were the first to study the genetic mechanism controlling spot color, by crossing yellow-spotted *P. polyxenes* larvae with orange-spotted *P. machaon* larvae, to produce orange-spotted hybrids. Clarke and Sheppard (1955b, 1956a) later showed that the hybrid larvae had spots which were a paler orange than those of *P. machaon*, and although yellow is recessive to orange, the degree of dominance of the orange allelomorph varies with the subspecies of *P. machaon*, They suggested that inheritance was controlled by more than one allele which could produce orange spots, or through modifiers at another locus. Clarke *et al.* (1977) established that the main locus controlling larval spot color was not linked to the locus controlling black and yellow wing morphs in adults.

P. machaon, *P. zelicaon*, *P. polyxenes* and *P. indra* are to some extent all polymorphic for larval spot color. Thus, this polymorphism probably predates the most recent common ancestor of these species. Nonetheless, differences in spot color have been used to support some taxonomic distinctions. For example, Remington (1968a) considered the fact that he had found and reared only yellow-spotted larvae of *P. gothica* as evidence contributing to his decision to name it as a separate species. His sample was comprised of few independent observations and provided little support for his decision, considering that most populations of *P. zelicaon* were known to produce both yellow and orange spotted larvae (Clarke and Sheppard, 1970). All 34 late-instar larvae which I found at Gothic had yellow spots, supporting Remington's observation of apparent allelic homogeneity at that locality. It would be interesting to determine if larvae of *P. zelicaon* in central Colorado generally have yellow spots and if their proportion decreases in populations farther away from *P. polyxenes*.

In western Canada, many samples from single localities contained a mixture of both yellow-spotted and orange-spotted larvae, but there were also a number of interesting frequency shifts between different taxa and between different regions (Figures 23–24).

The largest differences in frequency of spot color occurred within *P. machaon*. All larvae collected on *Artemisia dracunculus* in southern and central British Columbia had yellow spots, while in southern Alberta and Saskatchewan 99.6% had orange spots. Thus *P. m. dodi* and *P. m. oregonius* may have undergone a complete allele substitution over much of their range in western Canada. I do not know what the predominant spot color is where these races contact each other in the western United States.

In the Peace River region 28% of the larvae of *P. m. pikei* had yellow spots. If spot color is controlled by a single gene with orange dominant over yellow, then the Peace River *A. dracunculus*-feeding populations have a 50:50 ratio of these two alleles, making them exactly intermediate between *P. m. dodi* and *P. m. oregonius*.

There were far more yellow-spotted larvae in *P. m. aliaska* than in *P. m. pikei*, since 95% of the larvae collected on *A. arctica* had yellow spots. The single larva of *P. m. hudsonianus* which was scored (from a photograph by G. Anweiler) also had yellow spots. Thus *P. machaon* is clearly polymorphic for spot color in North America, but different ecological and geographic races have major frequency differences in spot color.

Samples of larvae collected on umbellifers in almost all localities from Alberta and British Columbia were polymorphic for spot color. Hence geographically separate populations of *P. zelicaon* and its hybrids may have quite different frequencies of spot color, as in *P. machaon*. However, the frequency shifts seem to be somewhat more clinal. Also, *P. zelicaon* larvae consistently had different spot color frequencies from *P. machaon* where these species have low hybridization rates. In Interior British Columbia and the Peace River region, *P. zelicaon* larvae had more orange spots, while in southern Alberta they had more yellow spots.

Hybrid populations did not show much difference from parent species. In central Manitoba, most of the larvae had yellow spots, while *P. polyxenes* larvae generally have yellow spots farther to the southeast, and the only known larval *P. m. hudsonianus* also had yellow spots. In central Alberta the northern populations have mostly orange spots and in this respect merge into the *P. zelicaon* populations farther to the north and west. This trend is mirrored in the adult morphometric and electrophoretic characters of these populations.

The shift toward predominantly yellow spots in the *P. zelicaon X machaon* hybrid swarm west of Calgary is more abrupt. Also, it is interesting to note that the only larva found on *Heracleum* at Bragg Creek had orange spots, while 42 of 44 on *Zizia* had yellow spots. *Heracleum* is a much more common foodplant for *P. zelicaon* populations immediately to the west, and larvae of these populations may have developed from eggs laid by a typical *P. zelicaon* that strayed in from the west. The fact that *P. m. dodi* larvae almost always have orange spots, even at the outer edges of the range of this subspecies, distinguishes the latter from the southern hybrid populations. This supports the contention that hybrid populations are the result of hybridization of *P. zelicaon* with races similar to *P. m. hudsonianus*, rather than to *P. m. dodi*.

ECOLOGICAL CHARACTERISTICS

Geographic Distribution and Habitat

The *Papilio machaon* group has a generally Holarctic distribution. Of the eight species recognized, four are restricted to North America, *P. alexanor* and *P. hospiton* occur only in western Eurasia, and *P. machaon* spans both continents. *P. polyxenes* is found mainly in North America, but is the only species that also occurs in South America.

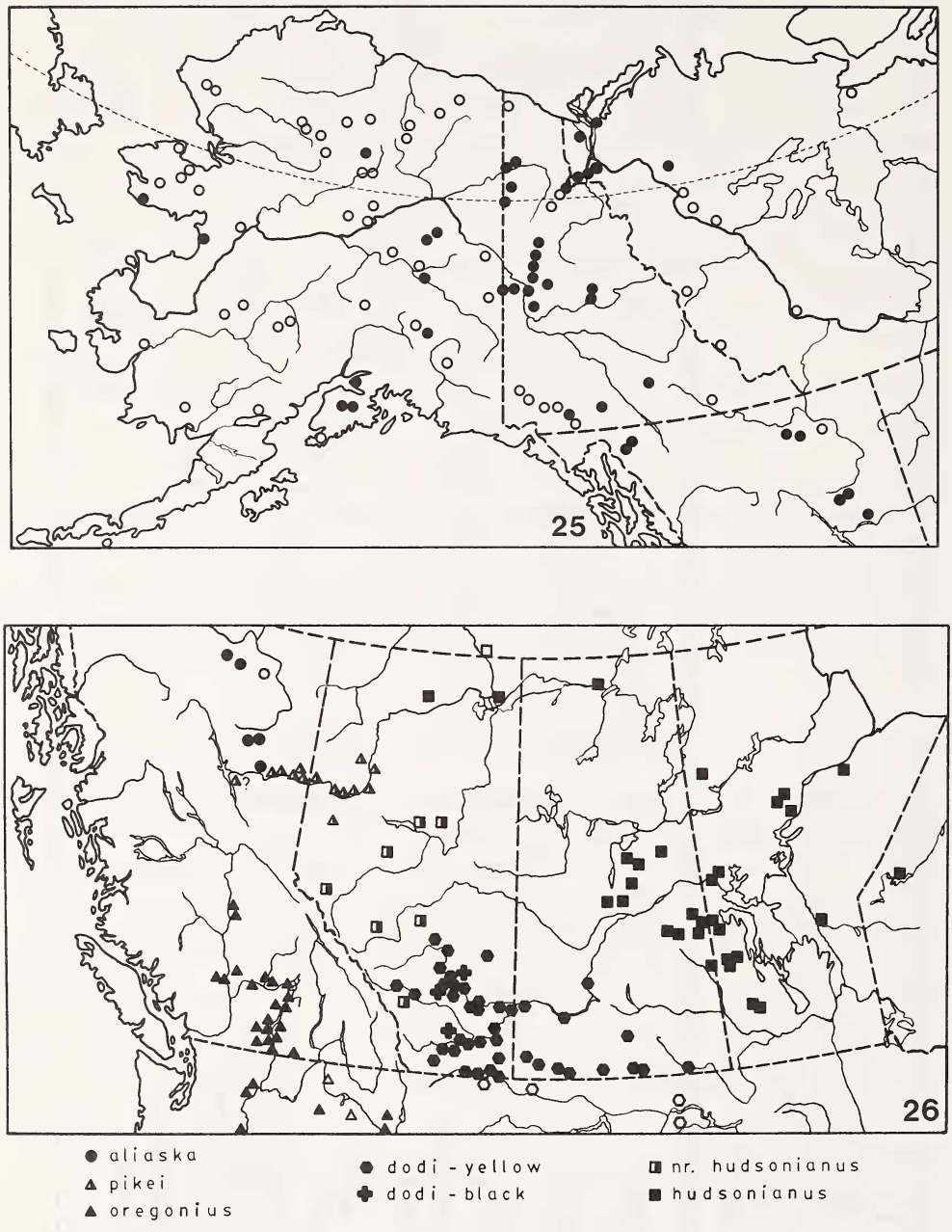
Species of the *P. machaon* group which have broad ranges also show a considerable diversity of habitat use. For example, different populations of *P. machaon* occur in habitats varying from cool temperate wetlands (Wiklund, 1974; Dempster and Hall, 1980) to hot Saharan deserts (Larsen, 1980), and in Nepal two distinct races are separated only by a continuous cloud belt (Dierl, 1976). Such varied habitat use may occur with relatively little evidence of regional morphological differentiation, as in mountain- versus prairie-adapted populations of *P. zelicaon*.

The three species of the *P. machaon* group living in western Canada interact in a complex pattern of geographic overlap, replacement along contact zones, and varying frequencies of hybridization (Table 9). *P. machaon* has five subspecies in this area, and is the only species which is represented by more than one subspecies. The subspecies of *P. machaon* are all either allopatric with each other, or parapatric but with very limited opportunities for gene flow (Figures 25 and 26). *P. m. hudsonianus* is rare in northern Alberta and northwestern Saskatchewan (*e.g.*, Bird *et al.*, 1982), and there is little opportunity for contact with either *P. m. aliaska* or *P. m. pikei*. *P. m. dodi* and *P. m. oregonius* are separated from the northern subspecies and, in Canada, from each other.

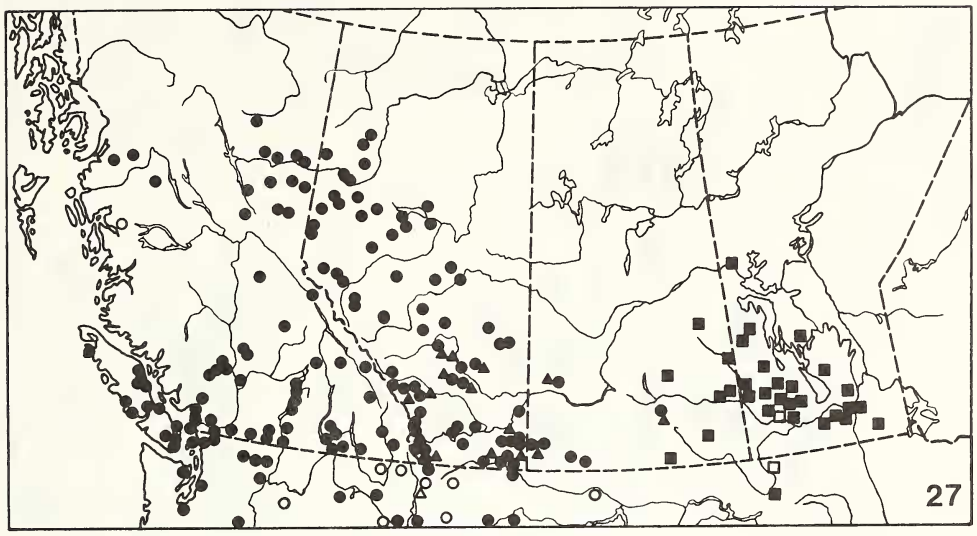
Table 9. Geographic contact between taxa and hybrids of the *P. machaon* group and frequency of black morphs in western Canada.

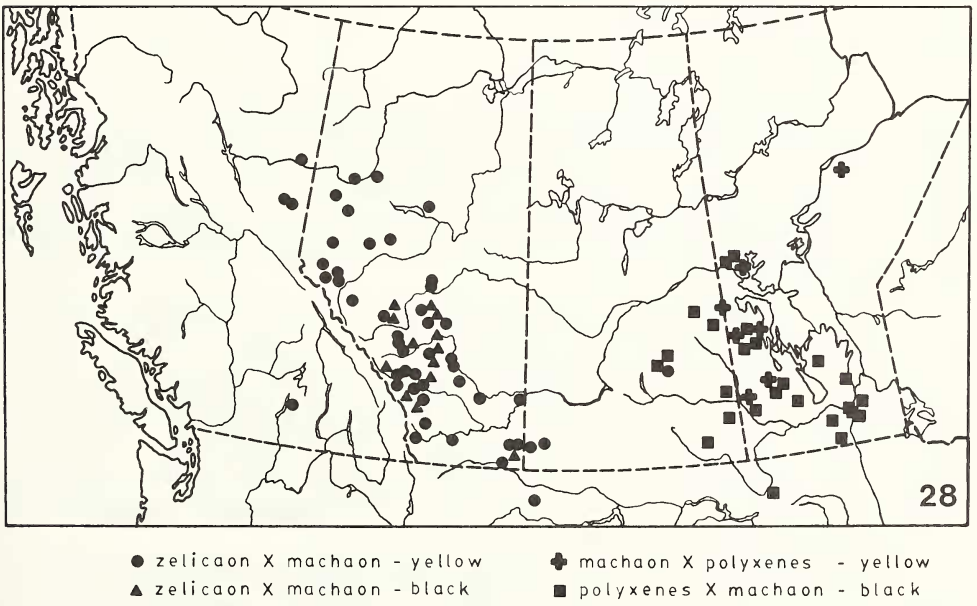
S = sympatry, with habitat segregation
P1 = abrupt geographic replacement, with low frequency of hybrids
P2 = separated by zone of low population density
P3 = clinal merging of populations
A = allopatry, with disjunction of more than 100 km

	Taxa and Hybrids	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	Black Morph
1.	*P. m. aliaska*												0
2.	*P. m. hudsonianus*	P2											0
3.	*P. m. pikei*	P1	P2										0
4.	*P. m. oregonius*	A	A	A									0
5.	*P. m. dodi*	A	A	A	A (P3 in western U.S.)								2%
6.	*P. zelicaon* X *machaon* -central Alberta	A	P2	A	A	P1							0 (north) to 12% (south)
7.	*P. zelicaon* X *machaon* -Cypress Hills	A	A	A	A	P1	A						approx. 12%
8.	*P. zelicaon* -southern British Columbia	A	A	A	S	A	P1	A					0
9.	*P. zelicaon* -Peace River region	P1	P2	S	A	A	P3	A	P3				0
10.	*P. zelicaon* -southern Alberta & Sask.	A	A	A	A	S	P1	P3	P3	P2			5-15%
11.	*P. polyxenes* X *machaon* -central Manitoba	A	S	A	A	A	A	A	A	A	P2		approx. 97%
12.	*P. p. asterius*	A	P1	A	A	P2	A	A	A	A	P2	P3	100%



Figures 25 and 26. Empty symbols indicate unverified published records. Figure 25. Distribution of *P. m. aliaska*. Figure 26. Distribution of *P. machaon* in western Canada.





Figures 27 and 28. Figure 27. Distribution of *P. zelicaon* and *P. polyxenes asterius* in western Canada. Empty symbols indicate unverified published records. Figure 28. Distribution of interspecific hybrids in western Canada.

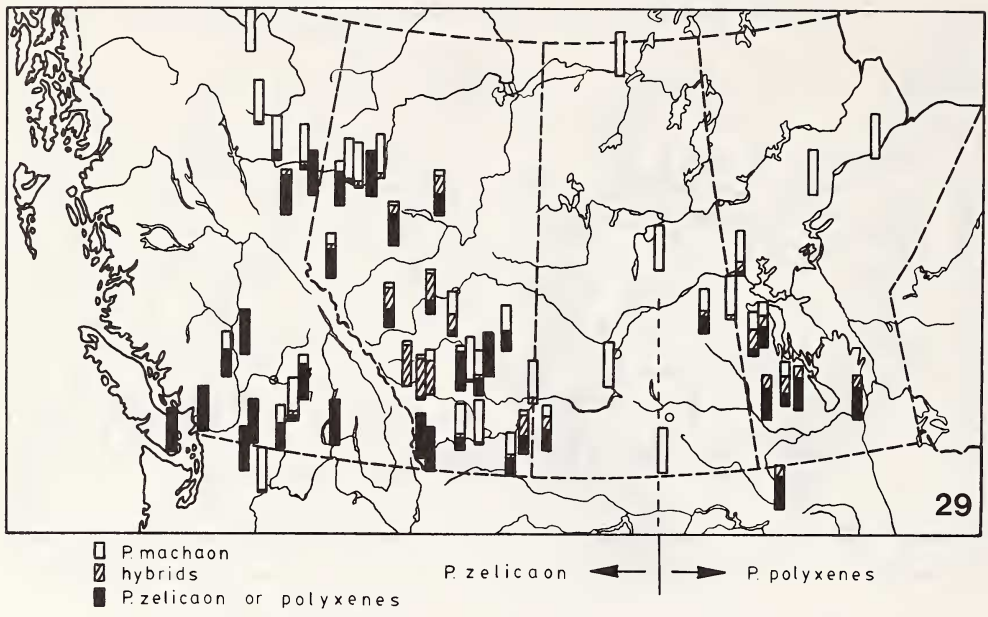


Figure 29. Frequency of interspecific hybrids in western Canada.

Papilio machaon occurs in most of the available major vegetation zones in western Canada (Figures 30 and 31), as shown by relating long term records for temperature and precipitation (Canadian Climate Normals, 1951–1980. [1982a and 1982b]) for weather stations close to localities at which specimens have been collected. These show a clear pattern of differing habitat use among the subspecies of *P. machaon*, as well as between *P. machaon* and the other two species (Figure 32 and 33).

P. m. dodi, *P. m. oregonius* and *P. m. pikei* are most common in patchy populations in dry valley bottoms and slopes of river banks or badlands. They are replaced by *P. zelicaon* at higher altitudes and in moister habitats (*e.g.*, McDunnough, 1927), though males of the two species are occasionally collected together on hilltops immediately surrounding dry valleys. *P. m. aliaska* is replaced by *P. zelicaon* in forested areas south of the Peace River, although *P. zelicaon* is not a resident in alpine habitats and only a few individuals fly to the tops of the lower mountains. According to Freeman (1972), the northern populations of *P. machaon* are also absent from areas with acidic granitic formations.

In contrast to the situation within *P. machaon*, populations of *P. zelicaon* are relatively continuous, with no evidence of any major disjunctions within the species (Figure 27). *P. zelicaon* occurs in broad sympatry with *P. machaon*, with a frequency of less than 5% of natural hybrids in much of western Canada (Figure 29), but large hybrid populations occur in south and central Alberta.

The Cypress Hills of southeastern Alberta and southwestern Saskatchewan contain one major hybrid population (Figures 28 and 29). *P. zelicaon* is found on the partially wooded and prairie hills surrounding the plateau, sometimes together with *P. m. dodi*, but both species merge into a hybrid population in the more heavily wooded central areas. The "Cypress Hills

Old World Swallowtail" (misidentified as *P. m. dodi*) of Hooper (1973), most likely refers to this hybrid swarm material.

A much larger series of hybrid populations is in central Alberta – probably the result of genetic swamping of a *P. m. hudsonianus*-like population which once existed in this region (Figure 42 and 44). *P. zelicaon* abruptly replaces the hybrid swarm populations west of the easternmost slope of the Rockies in Alberta, as well as south of the Crowsnest Pass. Near Lesser Slave Lake, at the northern edge of the central Alberta hybrid swarm, hybrid specimens form 20 to 40% of the total population at any one locality. This frequency increases toward the south and reaches a maximum west of Calgary, where specimens assigned as hybrids comprise more than 90% of the total populations (Figure 29). I have noticed no difference in habitat between individuals which are the most *P. zelicaon*-like, and those which are the most *P. machaon*-like ("nr. *hudsonianus*" in Figure 26). Almost all the localities at which hybrid populations are found occur between 1000 and 2000 m elevation in central Alberta, while localities recorded for *P. m. dodi* are below 1100 m (Figure 11). Hybrid forms are less common farther south and east of Calgary, probably because the foothills and mixed forest habitat they occupy is greatly reduced in extent. A few hybrid specimens from Bragg Creek and Buck Lake seem likely to have been derived in part from *P. m. dodi*. These adults have the long tails and pointed forewings which usually distinguish *P. m. dodi* from both *P. m. hudsonianus* and *P. zelicaon*.

P. polyxenes occurs in Manitoba, where the species fills part of the gap between boreal *P. m. hudsonianus* and prairie *P. m. dodi* and *P. zelicaon* (Figures 26 and 27). *P. polyxenes* X *machaon* populations from central Manitoba occupy a habitat very similar to that of *P. zelicaon* X *machaon* populations from central Alberta (Figures 28 and 33).

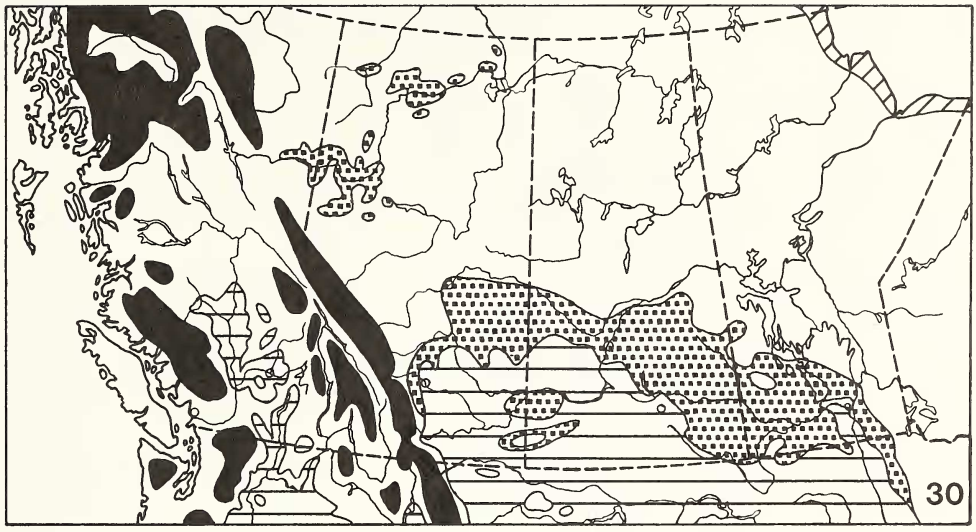
The hybrid populations in central Manitoba are for the most part isolated from the main range of *P. m. hudsonianus* and may be in the process of being swamped by *P. polyxenes* in the area, along with the remnants of *P. m. hudsonianus*. Most typical *P. m. hudsonianus* adults were collected in Riding Mountain Park in the 1930's and 1940's, at which time they appeared to form about half of the catch of local collectors. By 1955 *P. m. hudsonianus* was already quite uncommon (Remington, 1956), and in the mid 1970's it was certainly very rare (Heron and Robinson, 1976). Intermediate black morph adults also may be becoming less common, since they were at least as common as more typical *P. polyxenes* in the 1930's to 1950's, but have formed a lower proportion of the total catch in the last two decades. As well, specimens closer to the typical appearance of *P. p. asterius* are more common in the farmland, which surrounds Riding Mountain Park completely and Duck Mountain Park on three sides. Hybrid specimens are very rare north of Duck Mountain Park (Figure 16). The changing status of the hybrid populations in central Manitoba is a major reason for retaining the established taxonomic practice of recognizing these taxa as separate species.

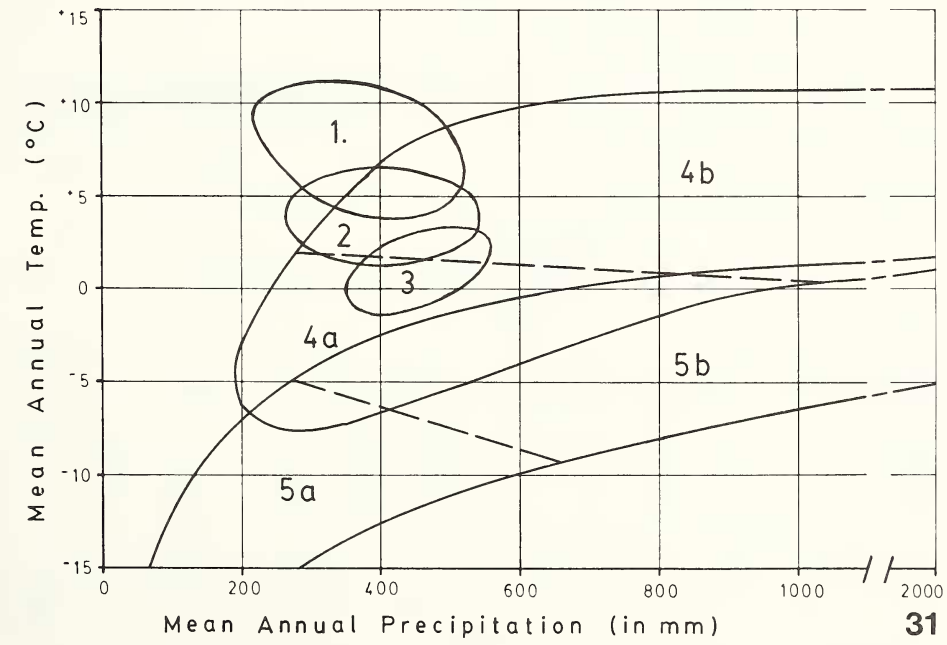
P. p. asterius is very uncommon in southern Saskatchewan, and so there is little contact with *P. zelicaon* in Canada. In Colorado, *P. polyxenes* occurs at lower altitudes than *P. zelicaon*, though these two species meet and occasionally hybridize along a broad zone of contact (Remington, 1968b; Fisher, 1980; Scott, 1981). In Missouri, *P. polyxenes* completely surrounds the range of *P. joanae*, and apparently these two species are reproductively isolated, in part by habitat preferences (Heitzman, 1973). Since *P. polyxenes* and *P. joanae* are distinguished by very few morphological characteristics, this contention of isolation is clearly in need of confirmation. Since the problem has not been investigated in the present study, I follow current practice (Opler and Krizek, 1984), and refer to *P. joanae* as a separate species.

Table 10. Flight periods in western Canada

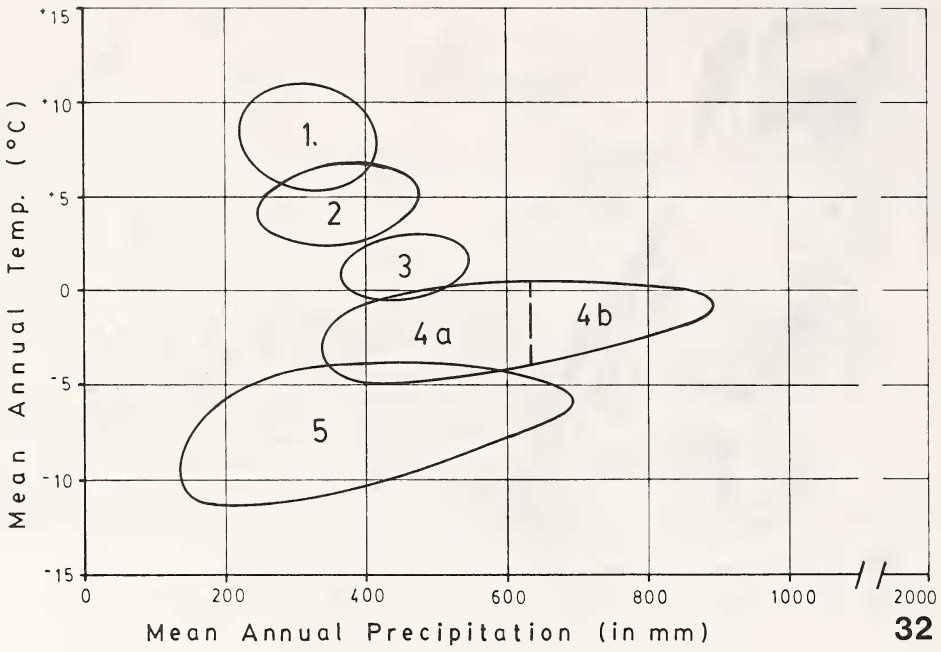
X = peak, + = reduced numbers, - = rare, ? = questionable record.

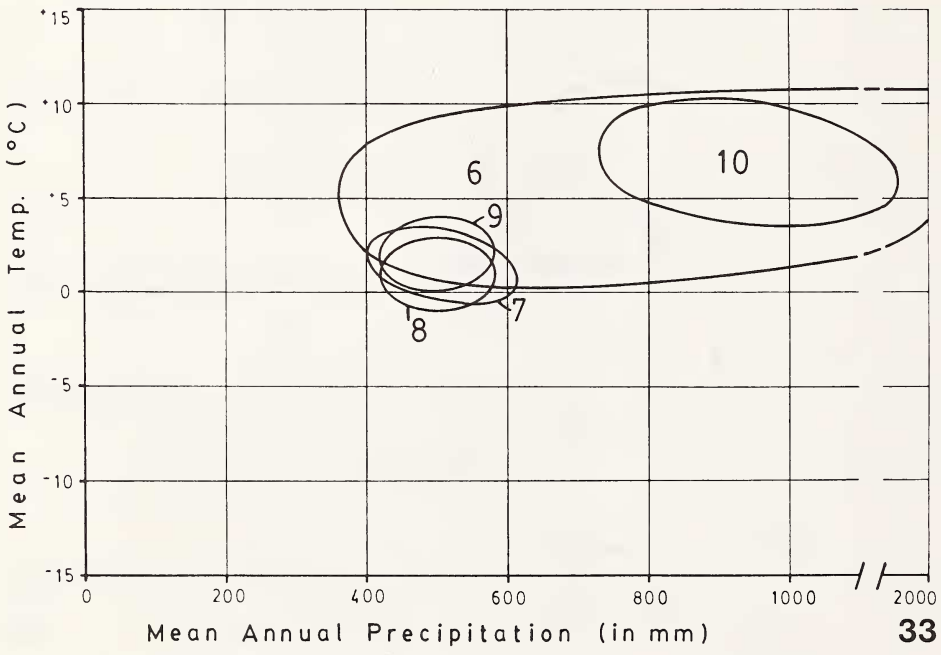
Taxon	April				May				June				July				August				September			
P. machaon aliaska								-		+	X	X	X	X	+	-		?	?					
P. machaon hudsonianus							-	-	-	+	X	X	X	+	-	?								
P. machaon pikei										X	X	X	+	+							?			
P. machaon dodi					-	+	X	X	X	+	+	+	-	-	+	+	X	-	-					
P. machaon oregonius			-	-		-	+	+	-	-	-	-	-	+	X	X	+	+	-					
P. zelicaon X *machaon* - central Alberta							-	+	X	X	X	+	+	+	-	-	-							
P. zelicaon X *machaon* - Cypress Hills							-	-		-	+	+	X	+	-			-						
P. zelicaon - southern British Columbia	-	-	-	+	+	-	X	+	+	+	+	X	+	+	+	-	-	-		-	-	-		
P. zelicaon - Peace River region							-	+		+	X	+	+	+										
P. zelicaon - southern Alberta prairie					-	+	+	X	-	-				-	-			-	-					
P. zelicaon - southern Alberta mountains					?	?				-	-	X	X	+	-	-	-	-	-					
P. polyxenes X *machaon* - Manitoba						-	-	-	+	X	X	X	+	-	-	-	-	-	-					
P. polyxenes asterius - Manitoba							+	+	X	X	X	+	-	-	+	+	-	-	-					
Bragg Creek: nr. *P. machaon*									-	+														
P. zelicaon X *machaon*							-	+	X	X	X	+	-	-			-							
nr. *P. zelicaon*								-	+	+	-	-	-	+	-	-	-	-	-					





Figures 30 and 31. Figure 30. Major vegetation zones in western Canada Figure 31. Mean annual temperature and precipitation of major vegetation zones Canadian Climate Normals, 1951-1980 (1982a and 1982b). 1, Grassland in southern British Columbia. 2, Grassland in southern Alberta and Saskatchewan. 3, Aspen parkland of Alberta to Manitoba. 4a, Boreal forest of northern British Columbia to Quebec. 4b, Forest of south and central British Columbia. 5a, Arctic tundra of Northwest Terr. to Quebec. 5b, Alpine tundra of Alberta, British Columbia and Yukon Territory.





Figures 32 and 33. Figure 32. Occurrence of *P. machaon* subspecies vs. mean annual temperature and precipitation: 1, *P. m. oregonius* in southern British Columbia. 2, *P. m. dodi* in southern Alberta and Saskatchewan. 3, *P. m. pikei*. 4a, *P. m. hudsonianus* in Alberta to Manitoba. 4b, *P. m. hudsonianus* in Ontario and Quebec. 5, *P. m. aliaska*. Figure 33. Occurrence of *P. zelicaon* and *P. polyxenes* vs. mean annual temperature and precipitation 6, *P. zelicaon* in Alberta and British Columbia; 7, *P. zelcaon* X *machaon* in central Alberta; 8, *P. polyxenes* X *machaon* in central Manitoba; 9, *P. p. asterius* in southern Manitoba; 10, *P. p. asterius* in eastern Canada.

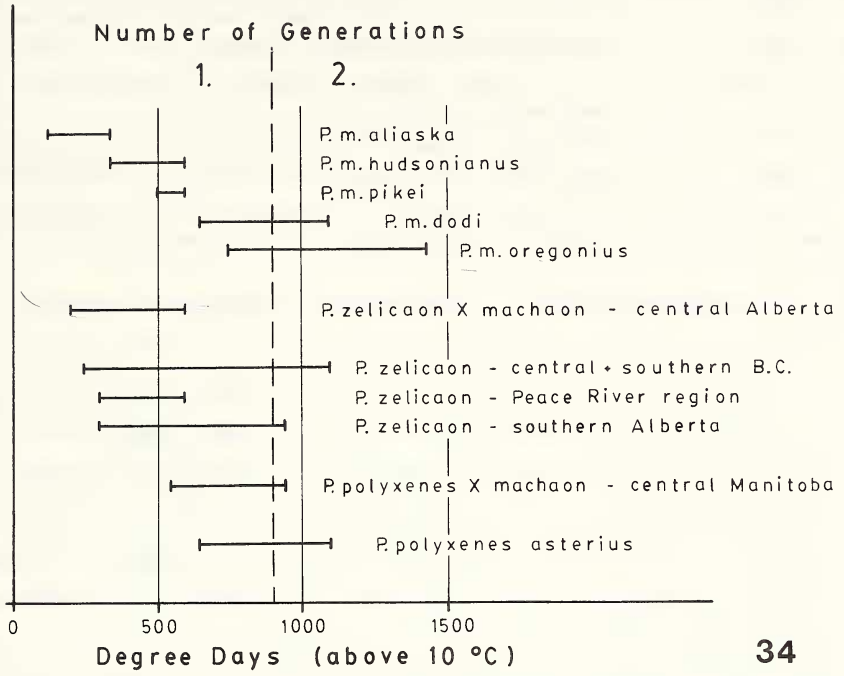


Figure 34. Relationship between voltinism and degree days. Bars show range of degree days (above +10 C) to which *P. machaon* group taxa are exposed in western Canada. Data are taken from weather stations near collection localities (Canadian Climate Normals, 1951-1980. [1982c]). Dashed line indicates approximate number of degree days above which populations have a partial second brood.

Phenology

Variation in flight period and voltinism in the *Papilio machaon* group is primarily geographic and within species. *P. machaon*, *P. zelicaon*, and *P. polyxenes* each include a variety of different populations which range from strict univoltinism to multivoltinism, and have a flight period for adults which ranges from a few weeks per year to an almost or completely continuous emergence (Blau, 1981a, 1981c; Dornfeld, 1980; Emmel and Emmel, 1973; Fisher, 1980; Wiklund, 1973; Wiltshire, 1958). The remaining species in the *P. machaon* group also have fairly flexible phenologies. Some populations of *P. indra* and *P. hospiton* are partially bivoltine (Fisher, 1980; Kettlewell, 1955). These two species and *P. alexanor* may have a very extended emergence period, depending on climatic conditions, and some pupae of *P. indra* and *P. alexanor* have remained in diapause for several years (Fisher, 1980; Nakamura and Ae, 1973). Since most species in the *P. machaon* group exhibit labile phenological responses to different habitats, the genetic potential to adjust in these ways is probably plesiotypic (ancestral) within the species group.

Phenological variation in the *P. machaon* group species is less pronounced in western Canada (Table 10), perhaps due to a more limited range of habitats. *P. machaon* and *P. zelicaon* are strictly univoltine in the northern regions of western Canada, and have a large second generation in the warmer southern regions (Figure 34). Partial bivoltinism is more widespread in southern *P. machaon* than in *P. zelicaon*, probably because the *P. machaon* populations occupy warmer habitats. *P. polyxenes* is at least partly bivoltine through most of its range in western Canada, but also shows a marked decrease northward in the size of the second generation, even though it occupies the relatively warm agricultural areas. The main flight period tends to occur slightly later in the year at higher altitudes and latitudes for all three species.

Although *P. zelicaon* adults tend to emerge slightly earlier in the season than those of *P. machaon* where these species are sympatric, the amount of overlap in flight period is still very large and cannot account for any interruption in gene flow between the species. A substantial amount of overlap in flight periods is also true of *P. machaon* and *P. polyxenes* in Manitoba.

Voltinism of *P. machaon* group populations is related to growing temperatures in western Canada. Figure 34 shows the approximate range of degree days above 10 C (Canadian Climate Normals, 1951–1980. [1982c]) to which these different populations are exposed. Populations which have some adults emerging in a second brood occur in areas receiving approximately 900 or more degree days per year. This contrasts with the situation in *P. glaucus*, in which the potential for multivoltinism appears in populations from areas receiving more than 1200 degree days per year (Scriber, 1982).

Despite similarities among related species with respect to phenologies, many artificial interspecific hybrids in *Papilio* show unusual characteristics of adult emergence. These can be relatively pronounced even when both species are within the same species group (Clarke *et al.*, 1972 and Oliver, 1969), as well as when they are more distantly related (Shimada, 1979). Natural hybrids of the *P. machaon* group in western Canada usually fly at the same time as the main flight of the parental species. However, several interesting exceptions are noted. In the grasslands of both the Peace River region and southern Alberta, where hybrids are rare, the latest record for any *P. machaon* group individual is for a hybrid specimen.

In central Manitoba, *P. p. asterius* has a partial second brood, while *P. m. hudsonianus* is univoltine. Some black morph individuals of *P. polyxenes* X *machaon* have been collected during the second brood flight period, but yellow morph hybrid individuals are only known from the first brood. This provides evidence, independent of similarities in color pattern, that yellow morph hybrids represent only the most *P. m. hudsonianus*-like proportion of the central Manitoba hybrid populations.

In central Alberta, the most *P. machaon*-like and the most *P. zelicaon*-like individuals generally fly in about the same proportions through most of the flight period. However, at Bragg Creek *P. zelicaon*-like individuals occur at low frequency throughout the flight period, but include the only two specimens collected as late as mid August (Table 10). The most likely explanation for the occurrence of these individuals is that they have dispersed in from the more typical *P. zelicaon* populations in the mountainous Kananaskis area immediately to the west. Since most of the *P. zelicaon* adults west of Bragg Creek fly at least a month later than hybrid populations at Bragg Creek, there is a partial temporal isolation of these hybrid populations from the parental species.

Although phenological variation within species of the *P. machaon* group grades clinally from one region to another and is generally not useful for making taxonomic distinctions, *P. m.*

pikei shows some distinctive features. It differs from southern *A. dracunculus*-feeding *P. machaon* subspecies in that *P. m. pikei* is strictly univoltine, while some proportion of these southern populations emerges as a second generation. These differences are maintained when larvae of these subspecies are reared together in the laboratory. Also, adults of *P. m. pikei* emerge a relatively long time after the onset of warm temperatures, compared to *P. m. dodi*, *P. m. oregonius* and *P. m. aliaska*. This difference in emergence time is especially noticeable considering that *P. m. dodi* adults are out early in the flight periods of such species as *Oeneis uhleri* Reakirt and *Papilio glaucus* L. in southern Alberta, but *P. m. pikei* adults do not fly until after the main flight of these species in the Peace River region. A possible explanation for this is that the short growing season in the Peace River region provides strong selection against bivoltinism, while larval foodplants are more abundant or palatable later in the season.

Larval Food Plants

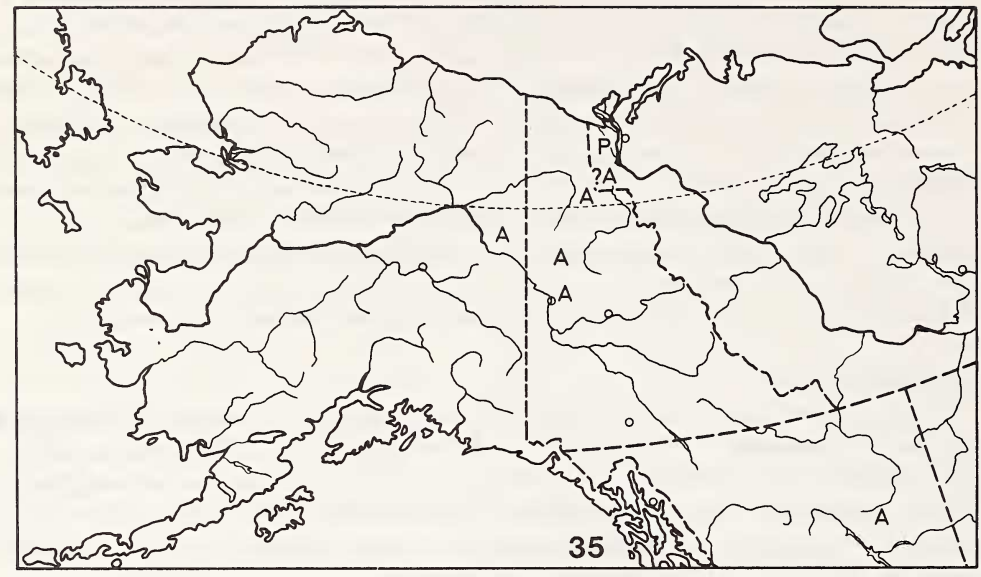
Larvae of the *P. machaon* group feed on a variety of species of Umbelliferae, Rutaceae and Compositae (Berenbaum, 1981; Emmel, 1975; Emmel and Shields, 1980; Higgins and Riley, 1970; Wiklund, 1974). Umbellifers are the most commonly recorded foodplants, though larvae of most species can feed opportunistically on rutaceous plants, and some populations of *P. machaon* have switched to composites. Within a restricted area, however, most larvae of a species are found only on one or a few species of foodplant.

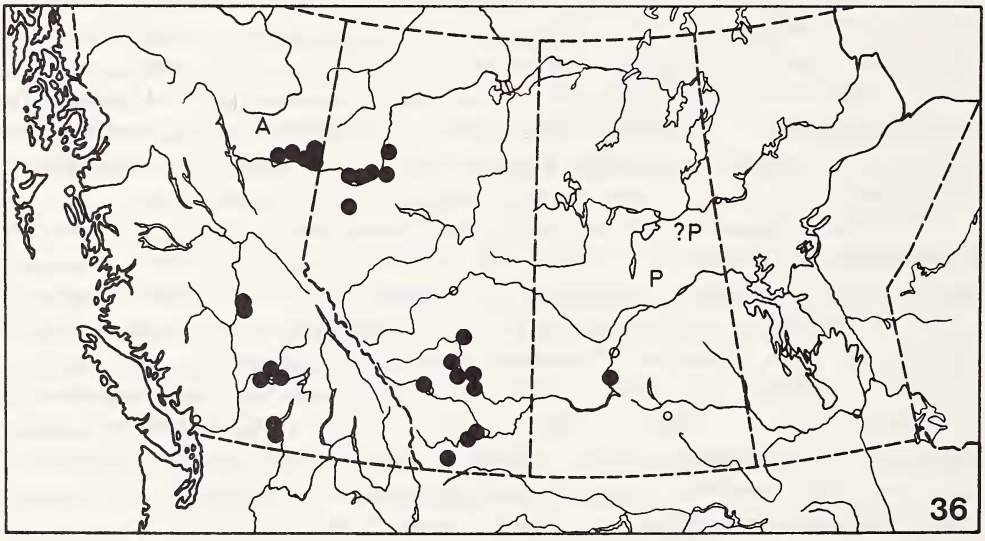
The ability to feed on rutaceous plants is widespread in the Papilioninae, and particularly in the genus *Papilio* (Ehrlich and Raven, 1964; Richard and Guédeès, 1983; Miller, 1986). Umbellifer-feeding species are restricted to *Papilio*, and are concentrated in the *P. machaon* group. Miller (1986) postulated that Rutaceae-feeding and Umbelliferae-feeding traits each arose at least three times in *Papilio*. On the other hand, the composite-feeding habits of *P. machaon* larvae are unique within *Papilio*. For the *P. machaon* group, I consider the composite-feeding habit to be the most derived trait, with umbellifer-feeding ancestral. The common ancestor probably evolved from Rutaceae-feeding stock, and Rutaceae-feeding habits have occurred as opportunistic reversals in several species of the *P. machaon* group.

Of the latter, larvae of *P. machaon* feed on the greatest range of foodplants. Records for Eurasian larvae of this species are mainly from umbellifers, less commonly from rutaceous plants, and only accidentally from plants of other families. An important exception occurs in northwestern Afghanistan, where Müting (1972) found mature larvae of *P. machaon centralis* Staudinger on "Wermutstrauchern" (*Artemisia absinthium* L.: Compositae). Larvae of North American subspecies of *P. machaon* appear to feed almost exclusively on composites, and particularly on plants of *Artemisia* (Figure 35 and 36). This contrasts with *P. machaon* populations from northeastern Siberia, which often occur in similar habitats, but for which Kurentzov (1970) mentions only various umbellifers as larval foodplants. Details about occurrence of larvae on foodplants are provided by Sperling (1986).

The only two records for wild-collected larvae of *P. m. aliaska* from North America are from composites (Table 14). Several other foodplant records for *P. m. aliaska* refer to ovipositions observed on *A. arctica* plants. A few larvae of *P. m. aliaska* may feed on umbellifers in nature (Kimmich, 1979), but no larvae have as yet been collected on umbellifers.

A single record of a wild-collected larva is known for *P. m. hudsonianus* (Table 14). I have seen a photograph by G. Anweiler of a freshly molted fifth instar larva resting on a leaf of *Petasites palmatus* (Compositae), with feeding signs on the side of the leaf. The plant represented a different variety of the same species on which Bryant found *P. m. aliaska* larvae





Figures 35 and 36. Locations of larvae collected on composites: A = *Artemisia arctica* Less; black dots= *Artemisia dracunculus* L.; P = *Petasites palmatus* (Ait.) Gray. Figure 35. *P. machaon* larval records – Alaska and Yukon Territory. Figure 36. *P. machaon* larval records – Western Canada.

at Aklavik (Leussler and Bryant, 1935). Anweiler also observed oviposition by *P. m. hudsonianus*, which was reported by Hooper (1973) as being on black snakeroot (Umbelliferae), but the record could just as well refer to *Petasites palmatus* (R. Hooper, *in litt.* 1981).

Many larvae of the *P. machaon* group have been found on plants of *Zizia aptera* (Umbelliferae) in central Manitoba. Though most of these developed into black morph adults (*P. p. asterius* or *P. polyxenes X machaon* hybrids), about 2% of them produced yellow adults similar to *P. m. hudsonianus* (*in litt.*, J. Troubridge). However, the yellow adults differed from typical *P. m. hudsonianus* in showing a basally darkened, *avinoffi*-like wing pattern that suggested they were hybrids with *P. polyxenes*. I have also reared adults very similar to *P. m. hudsonianus* from *P. zelicaon* X *machaon* hybrid populations at several localities on the east slope of the Rockies in Alberta. The foodplants included *Z. aptera* at Bragg Creek, and *H. lanatum* at Buck Lake and Nordegg.

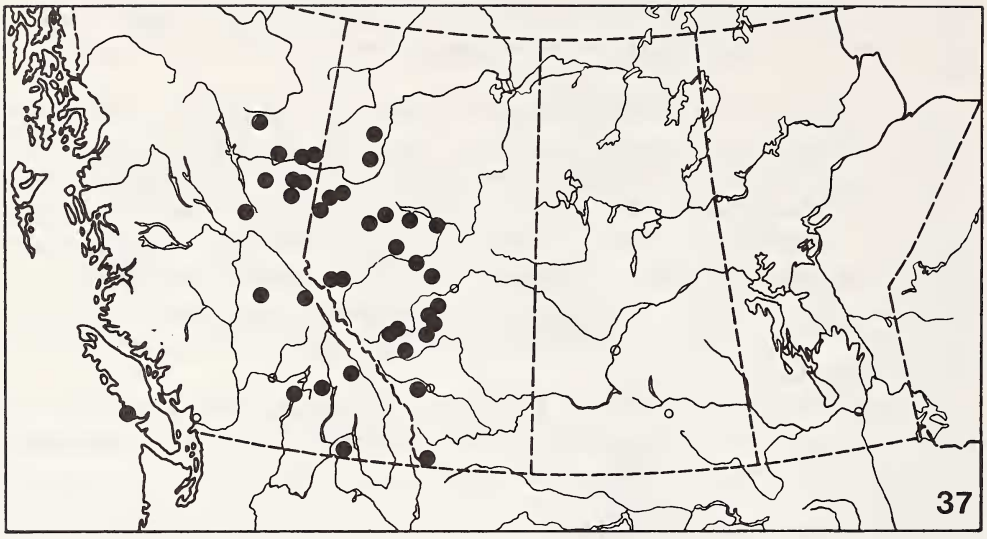
Although the southern subspecies of *P. machaon* have previously been considered to be specifically distinct from *P. m. aliaska* and *P. m. hudsonianus*, it is clear that the differences in larval foodplant between these taxa are relatively small. Larvae of *P. m. pikei*, *P. m. oregonius*, *P. m. dodi*, and *P. m. bairdii* are all restricted to a single species of Compositae, *Artemisia dracunculus* (Table 14). Many larvae of *P. machaon* collected on *A. dracunculus* feed on umbellifers if they are transferred to them (Edwards, 1893, 1898; Emmel and Emmel, 1963; J. Troubridge, *in litt.* 1981; personal observation, 1982; but contrast Newcomer, 1964). However, mortality of these larvae is high on most umbellifer species. Larvae of *P. zelicaon* and *P. polyxenes*, for their part, do not feed on *A. dracunculus*.

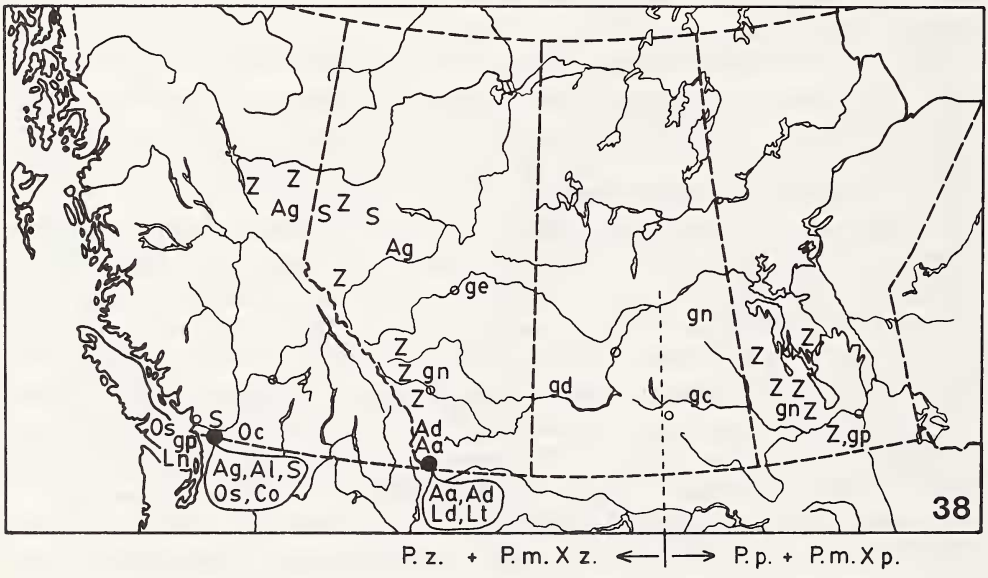
P. zelicaon larvae feed on rutaceous plants as well as on a wide variety of umbellifers in the United States, and *Angelica* species seem to be especially favored (*e.g.*, Emmel and Shields, 1980). In contrast, *P. indra* larvae are found on a narrower range of umbellifers, particularly *Lomatium* species (Emmel, 1975). Although largely separated by habitat, some *P. zelicaon* larvae feed on the same species of foodplants as those used by *P. indra* larvae.

In California, *P. zelicaon* larvae feed frequently on the introduced weedy umbellifer, *Foeniculum vulgare* Mill., and in some localities feed on *Citrus* (Rutaceae) orchards (Shapiro and Masuda, 1980). The foodplant shift to recently introduced umbelliferous and rutaceous plants has allowed *P. zelicaon* to produce several broods a year on these host plants, rather than the single brood that is normally possible on native umbellifers (Emmel and Shields, 1980; Sims, 1980 and 1983). Remington (1968a) considered larval foodplant preferences as evidence for the specific distinctness of his *P. gothica*. However, the foodplant preferences he listed have been disputed by Emmel and Shields (1980). I have confirmed the findings of the latter authors by obtaining larvae from plants of *Angelica ampla*. One larva was reared to the adult stage.

In western Canada, only umbelliferous foodplants are known for larvae of *P. zelicaon* (Table 14, Figures 37 and 38). *Heracleum* plants are used commonly, though *Angelica* plants tend to be used more frequently at localities where these plants are more numerous. Although plants of *Artemisia arctica* and *Heracleum lanatum* grow together near treeline at many sites in the Peace River region, this does not seem to promote hybridization between *P. zelicaon* and *P. m. aliaska*.

Larvae of *P. zelicaon* X *machaon* populations in central Alberta also feed on umbellifers. At Bragg Creek, these populations show some segregation from *P. zelicaon* populations to the west and south, and the larvae feed mainly on plants of *Zizia*. In the northern part of central Alberta, the hybrid populations merge into typical *P. zelicaon*, and the larvae feed on





Figures 37 and 38. Locations of larvae collected on umbellifers. Figure 37. Larvae collected on plants of *Heracleum lanatum* Michx. Figure 38. Larvae collected on other umbellifers. Aa = *Angelica arguta* Nutt.; Ad = *Angelica dawsoni* S.Wats.; Ag = *Angelica genuflexa* Nutt.; Al = *Angelica lucida* L.; Co = *Cicuta occidentalis* Greene; Ld = *Lomatium dissectum* (Nutt.) Mathias & Constance; Ln = *Lomatium nudicale* (Pursh) Coult. & Rose; Lt = *Lomatium triternatum* (Pursh) Coult. & Rose; Oc = *Osmorhiza chilensis* Hook. & Arn.; Os = *Oenanthe sarmentosa* Presl.; S = *Sium suave* Walt.; Z = *Zizia aptera* (A.Gray) Fern; gc = garden carrot (*Daucus carota*) L.; gd = garden dill (*Anethum graveolens*) L.; ge = garden celery (*Apium graveoens*) L.; gn = garden parsnip (*Pastinaca sativa*) L.; gp = garden parsley (*Petroselinum crispum*) (Mill.)Mansf.

Heracleum plants, a more common foodplant of *P. zelicaon.*

I have obtained black morph adults from two species of Umbelliferae: one, with typical *P. zelicaon* on *Angelica arguta* at Waterton Park, Alberta; others, on *Zizia*, and were part of the hybrid population at Bragg Creek, Alberta. In both groups the black and yellow morph specimens were produced in similar proportions to those of wild-collected adults. Hooper (1973) also reported both black and yellow morphs being produced from the same umbelliferous foodplant: garden dill (*Anethum graveolens*) at Eston, Saskatchewan. As well, I have reared one black morph adult from larvae of *P. m. dodi* , collected on *Artemisia dracunculus* at Taber, Alberta. These observations support the electrophoretic evidence, which indicates that the black adult morph is an integrated part of several taxonomically different *P. machaon* group populations in western Canada.

Larvae of *P. p. asterius* are found on a broad range of umbellifers and even a few rutaceous species (Berenbaum, 1981). Many of these are either introduced or common in cultivated areas, and so the fact that *P. p. asterius* is a common butterfly in much of eastern North America may be a recent phenomenon, aided by human agricultural patterns in the last two hundred years or so (Feeny *et al.*, 1985). Larvae of *P. p. asterius* may occasionally be found on the same species which support *P. joanae* and *P. brevicauda* and so these ecological distinctions between the two species are not major (Berenbaum, 1978; Jackson, 1982; Opler and Krizek, 1984). In desert areas of the southwestern United States, *P. p. coloro* Wright larvae feed mainly on plants of *Thamnosa* species (Rutaceae) (Ferris and Emmel, 1982). In this region *P. polyxenes* is in part sympatric with *P. m. bairdii* (larvae of which feed on *Artemisia dracunculus*), and *P. indra* (larvae of which feed on umbellifers).

As with *P. zelicaon* , the larvae of *P. p. asterius* feed only on umbellifers in western Canada. However, the larvae of *P. p. asterius* frequently use introduced and cultivated foodplant species, while this is more infrequent for *P. zelicaon* larvae. I have examined adult series reared from two introduced foodplant species in Manitoba and Saskatchewan (Table 14). Both of these series contain specimens ranging from typical *P. p. asterius* to at least one which was more typical of the *P. polyxenes X machaon* hybrid populations which are common in forested areas.

In the zone of interaction between *P. p. asterius* and *P. m. hudsonianus* in central Manitoba, the native umbellifer, *Zizia aptera*, is the primary larval foodplant (Figure 38). *Z. aptera* plants are more characteristic of open meadows than forests, and so are not a major factor in the partial habitat separation between hybrid populations of *P. polyxenes* and *P. polyxenes X machaon.* I have not been able to confirm Tyler's (1975) report that cow parsnip (*H. lanatum*[?]) may be a larval foodplant for these populations.

Table 11. Character state distributions within *P. machaon* group taxa

Frequency: X = most common, + = greater than 10%, - = less than 10%
Adult morph.: Letters and numbers correspond to those of characters on Table 2.
Adult electr.: Only alleles with a frequency of more than 10% in at least one taxon are included. Allele letters correspond to those in Table 6. Character polarities not shown due to absence of outgroup information.
Larval: Spot color (sp) = orange (o) & yellow (y). Foodplants (fd.) = Rutaceae (r), Umbelliferae (u) & Compositae (c)
Misc. abbrev.: P = primitive, D = derived, c.AB = central Alberta, c.MB = central Manitoba

CHARACTER SUITE	Adult Morphometric											Adult Electrophoretic								Larval	
CHARACTER NUMBER OR LETTER	A.	B.	C.	D.	E.	F.	G.	H.	I.	J.	K.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
CHARACTER NAME	DHW yel.	DHW pup.	DHW b/r	teg ula	VFW disc	VFW tip	VHW or.	tho rax	abd. VL	abd LL	abd. UL	G6PD	ID	ME	ODH	E4	E5	P1	P2	sp	fd.
STATE or ALLELE	1234	1234	123	123	1234	123	1234	123	1234	123	1234	abkc	bd	iab	abc	ab	ac	ab	ab	oy	ruc
P. hospiton	+X-	+X	X	X	X-	X	X+	X	X	X	X									X	X
Palearctic *P. machaon* ssp.	+X+-	X+	X+-	X	X-	X	X+	X	X	X	X									X	+X-
P. m. oregonius	-+X+	-X-	X++	X	X+-	X	+X-	X	X-	X	X	- X	X+	++X	-X	X	+X	X	+X	X	X
P. m. dodi	+X+	-X+-	-+X	X-	++X	X	-X--	+X-	+--X	X--	-X	---X	X+	-+X	-X	X-	+X	X-	+X	X-	X
P. m. bairdii	X++	X+	-+X	X+	-+X	X+	-X--	++X	---X	++X	X+-+									X+	X
P. m. pikei	X++	+X-	X+-	X	X	X	X+	X	X	X	-X	---X	X-	+X	X-	X-	X+	X+	-X	X+	X
P. m. aliaska	X-	X+	X+	X	X-	X	+X	X	X	X	+X	-- X	X+	-+X	-X+	X-	-X	X+	-X	-X	X
P. m. hudsonianus	X-	+X-	-+X	X	X--	X	+X	X-	X	X	+X+	-- X	X+	-+X	+X-	X+	-X	X+	-X	X	X
P. zelicaon X *machaon* -c.AB	X+-	-X+-	-+X	X-	+++X	X-	-X--	+X+	+--X	X-+	--+X	-+-X	X+	--X	+X-	X+	+X	X+	+X	+X	X
P. zelicaon	X++-	-+X	-X	X-	-+X	X	-X--	X+	--X	X--	--X	-X-+	X-	--X	-X-	-X	-X	X-	+X	+X	+X
P. pollyxenes coloro	X++-	-+X	X	+X+	X	X++	+X+	+X	X	+-X	X+--									?X	X-
P. polyxenes X *machaon* -c.MB	X-	X++	-+X	+X+	--X	++X	-+X	--X	---X	--X	X--	+- X	X+	++X	-X	X-	+X	X	XX	-X	X
P. p. asterius	X	-+X	X	+X	X	-X	X	X	X	X	X	X	X	-+X	X	X	X	X	X-	+X	-X
P. joanae	X	+X	X	-X	X	-X	X	X	X	X	X									-X	X
P. brevicauda	X	-+X	X	X-	X	+X-	X	X	X	X	X	X+ +	X	++X	X	X+	X	X	-X	-X	X
P.p.polyx.,stabilis &americus	+X+	+X	X	X++	--X	X++	X	-X	--X	-+X	X+-									X+	-X
P. indra	X-	-+X	-X	X+-	X	-X	X+	X	X	X+	X									X+	X
CHARACTER POLARITY	DPDD	DPPD	DDP	PDD	DPPD	PDD	PPDD	PDD	PDDD	PDD	DDDP									PD	PPD

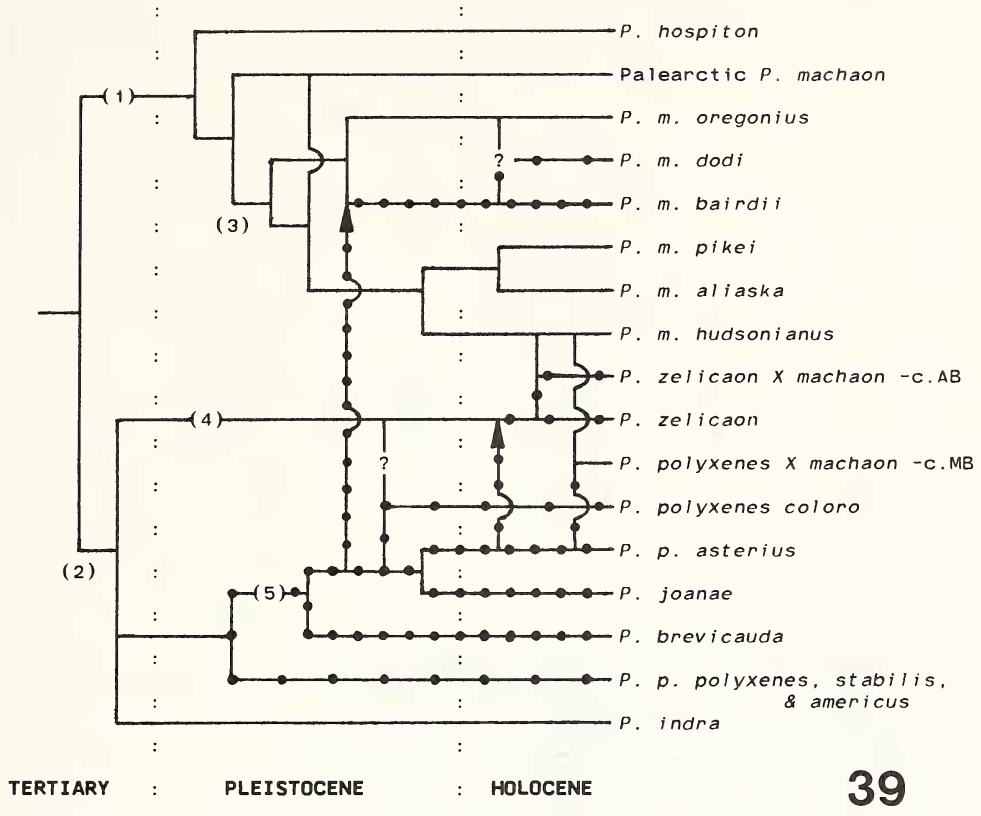


Figure 39. Reconstructed phylogeny of *P. machaon* group. Location of numbers shows hypothesized first appearance of derived states. Letter and number codes are the same as on Tables 2 and 11. Dots on lines represent spread of modifier gene for black wing morph. Widely spaced dots indicate low proportion of black morph individuals or incompletely linked gene combinations. Abreviations: c.AB = central Alberta; c.MB = central Manitoba; 1, B1, C1, E1; 2, A1, B4, E4, H2, I4; 3, 10c; 4, no autapotypies among characters analyzed; 5, D3, F3, G4, H3, J3, K1.

EVOLUTIONARY HYPOTHESES

Origin and Early Differentiation of the *P. machaon* Group

Outgroup relationships of the *P. machaon* group are uncertain. Monroe (1961) did not resolve its affinities to other species groups of *Papilio*, but associated it with the *P. xuthus* group, and suggested that these two groups had affinities with the *P. demoleus* and *P. anactus* species groups. Ae (1979) suggested that the *P. machaon* group was about as closely related to the *P. xuthus* group as it was to the *P. paris* group, which Monroe did not include in his reconstructed phylogeny. Ae also showed that the affinities of the *P. machaon* and the *P. demoleus* groups were probably still more distant. Hancock (1983) ranked the *P. machaon* group as a distinct genus with only ancestral relationships to most of the remainder of the Papilionini. He also suggested that *P. alexanor* represented a lineage predating a split between the *P. machaon* group and more than half of the species groups in the Papilionini.

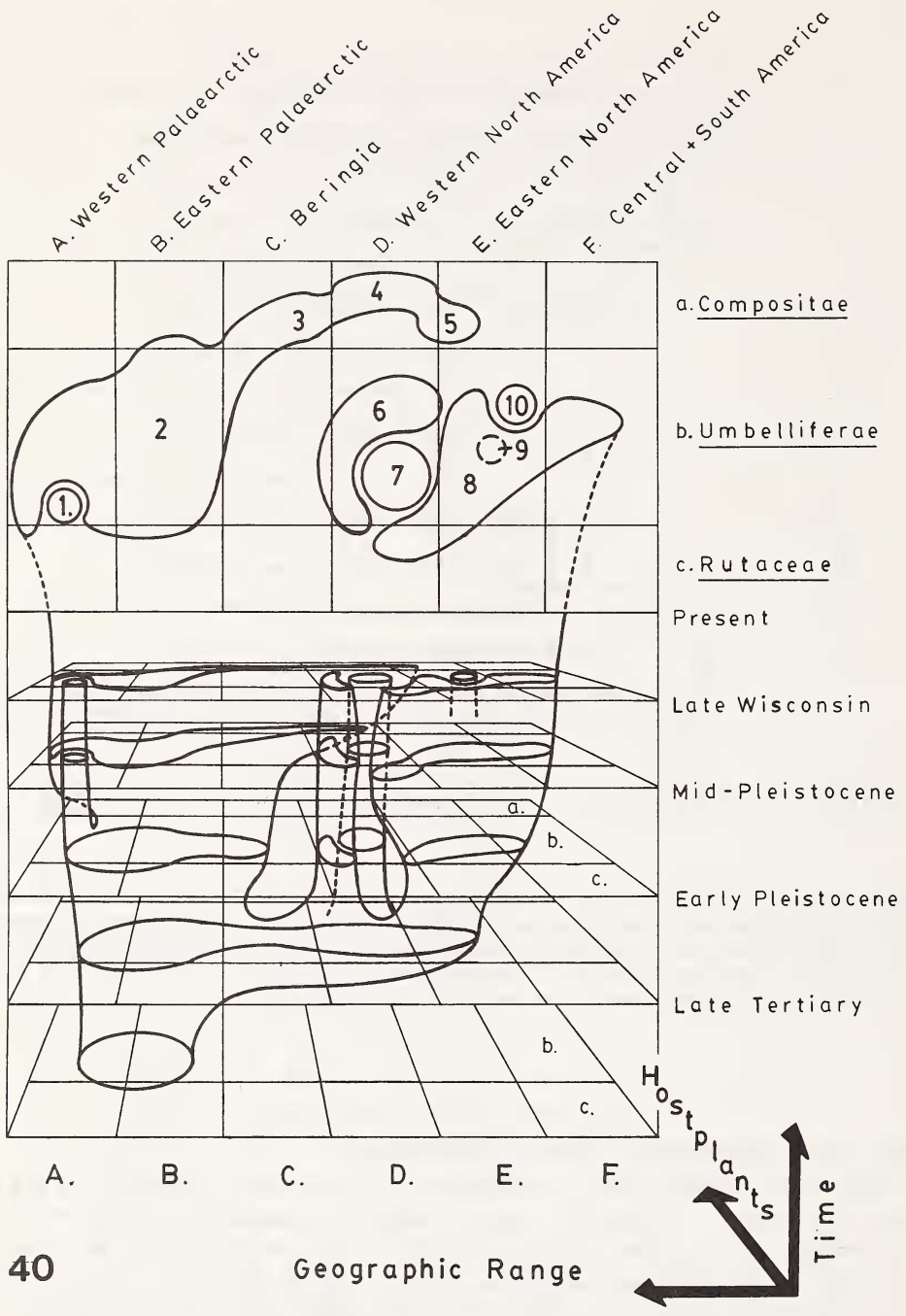


Figure 40. Changes in geographic range and larval hostplants over time: 1, *P. hospiton*; 2, Palearctic *P. machaon* ssp.; 3, *P. m. aliaska*; 4, *A. dracunculus*-feeding ssp. of *P. machaon*; 5, *P. m. hudsonianus*; 6, *P. zelicaon*; 7, *P. indra*; 8, *P. polyxenes*; 9, *P. joanae* (not shown in Late Wisconsin); 10, *P. brevicauda*.

Since adults of *P. alexanor* have a very different, and probably plesiotypic, color pattern and male genitalia, that species must have diverged early from the remainder of the *P. machaon* group. In fact, its inclusion in the *P. machaon* group on the basis of larval characters is so clearly contradicted by adult characters, that I consider it with some caution in my discussion of the phylogeny of the *P. machaon* group.

Because relationships of the *P. machaon* group are uncertain, it is difficult to determine which of its character states are plesiotypic. Seyer (1982) polarized character states by considering genetically dominant traits to have been more recently derived than traits which are more recessive. Since the allele for the black wing morph of *P. p. asterius* is dominant, it was considered derived relative to the yellow morph. On this basis Seyer concluded that *P. zelicaon* was phylogenetically older than *P. machaon*, *P. hospiton* and *P. polyxenes*.

Despite the uncertainty involved in such an undertaking, I offer a hypothesis for the character states of the most recent common ancestor of the *P. machaon* group, excluding *P. alexanor*. My identification of character states as plesiotypic is mainly determined by similarity of these states to those occurring frequently in different possible outgroups. On this basis, the ancestral species was probably similar to present day *P. machaon* though differing in some respects (Table 11), which indicate affinities with either *P. hospiton* or *P. p. americus*. Since none of the possible outgroups occur in the New World, this ancestral species probably lived in the Palearctic region, though it must have dispersed to North America early in the development of the *P. machaon* group.

The ancestral species certainly lived before the Pleistocene, considering the amount of differentiation within the group, though I doubt that the present species in the *P. machaon* group (excluding *P. alexanor*) began to diverge from each other very long before the beginning of the Pleistocene (Figures 39 and 40). Nei's (1972) genetic distance (D) can be a rough indicator of the time of divergence of two lineages, with D increasing by 1.0 every 15–20 million years (Thorpe, 1982:153). Applying this ratio to a value of 0.2 for interspecific comparisons within the *P. machaon* group (Table 7), a divergence time of 4–5 million years is obtained for the three species now occurring in western Canada. For the subspecies within *P. machaon*, divergence times of 0.1 to 1.0 million years are indicated. Although these estimates are imprecise, they nonetheless support the contention that the main lineages of the *P. machaon* group diverged before the Pleistocene, while most evolution within lineages took place during the Pleistocene.

The species which appeared immediately prior to the Pleistocene probably gave rise to four major lineages in the *P. machaon* group, in addition to *P. alexanor*. These lineages include what are now: 1), *P. machaon* and *P. hospiton* ; 2), *P. zelicaon*; 3), *P. polyxenes* , *P. joanae* and *P. brevicauda* ; and 4), *P. indra*. The oldest of these four lineages is probably the one that gave rise to *P. machaon* (Figure 39 and 40). Both *P. hospiton* and *P. machaon* exhibit very few of the apotypic character states of the remaining lineages (Table 11). As well, it is more parsimonious to hypothesize that the *P. machaon* lineage evolved *in situ* in Eurasia, and is not the product of a return dispersal from North America. However, the common ancestor of the remaining lineages probably fragmented soon after colonizing North America. Both electrophoretic characters (Table 7) and hybridization in the laboratory (Ae, 1979) indicate that *P. machaon* , *P. zelicaon* and *P. polyxenes* are approximately equidistant from each other. Also, natural hybridization occurs between each pair combination of these three species, as well as between *P. machaon* and *P. hospiton*.

Relationships of the three lineages which originated in North America are unclear. *P. zelicaon* possesses few if any autapotypic characters, and could conceivably represent the earliest of the three clades to diverge. However, *P. zelicaon* shows little internal differentiation. Although the color pattern of adults of *P. p. asterius* is probably apotypic, *P. polyxenes* contains other races and forms (particularly in *P. p. americus*) which appear to be more plesiotypic. *P. indra* , on the other hand, appears to share some apotypic character states with some subspecies of *P. polyxenes* (Table 11), but shows considerable internal differentiation, and has distinctive adult genitalia and adult and larval color patterns. Though this degree of differentiation may indicate an early divergence time relative to the other species, it may also be a reflection of a different sort of selection regime. In fact, it is conceivable that *P. indra* is so different only because some factor such as distinctive hilltopping behavior (Shapiro *et al.*, 1981) or male genitalia may have allowed it to avoid hybridization and introgression with other species, even though the lineage may be no older than the other three. Since it seems plausible that all three lineages could have diverged at the same time (in West Coast, American southwest, and eastern refugia), I have left this portion of the reconstructed phylogeny as a trichotomy. Further investigations on the species in the American southwest would be important to understanding phylogenetic relationships within the group.

Two main factors contribute to the obscure phylogenetic relationships within the *P. machaon* group. Species with extensive variation and large geographic ranges may simultaneously bud off two or more peripheral populations which are substantially different from each other. Reticulation due to interspecific hybridization is also likely to have been a significant factor in the evolution of the group. For example, the black wing morphs of *P. zelicaon* and *P. machaon* probably result from introgression of genes from *P. polyxenes*, while hybrid populations of two of the three potential combinations are described in this study. Both reticulation and multiple events of peripheral isolation in variable species are likely to produce discordant character distributions, with resultant difficulties in reconstruction of phylogenetic relationships.

Pleistocene Divergences Within Major Lineages

The first dispersal of the *Papilio machaon* group into North America almost certainly took place across the Beringian region between eastern Siberia and Alaska. Land connections through Beringia were intermittent during the Tertiary, and these also formed an intermittent but important biotic dispersal corridor during the Pleistocene (Matthews, 1979).

Large scale glacial advances and retreats that occurred throughout the Pleistocene must have been an important factor in differentiation of new species and races. These glaciations, combined with dramatically altered climates, moved many vegetation associations far south of their present ranges and caused formation of some vegetation associations which have no modern analogs (Matthews, 1982). Glaciations would have displaced populations of the *P. machaon* group a number of times, isolating those in Beringia, and probably fragmenting populations which survived south of the ice in North America.

Distributions of vegetation associations during and after the late Wisconsinan have been fairly well documented. I assume that the habitat associations of most *P. machaon* group taxa have not changed greatly since this time, and thus infer which regions were occupied by these taxa during late Wisconsinan time. Locations of these hypothetical refugial areas are shown in Figure 41, based in part on Scudder (1979:159).

Figure 41. Locations of late Wisconsinan refugia. Continuous lines indicate ice masses. Broken lines show refugia hypothesized for *P. machaon* group taxa in the United States and Canada: 1, *P. m. aliaska*; 2, *P. m. oregonius*; 3, *P. m. hudsonianus*; 3a, *P. machaon* populations similar to *P. m. hudsonianus*, remnants present in *P. zelicaon* X *machaon* hybrid populations in central Alberta; 4, *P. zelicaon*; 5, *P. m. bairdii* and *P. p. coloro*; 6, *P. p. asterius* and *P. joanae*(?); 7, *P. brevicauda*.

Figure 42. Distribution of *P. machaon* in North America. Arrows show hypothesized Holocene dispersal routes.

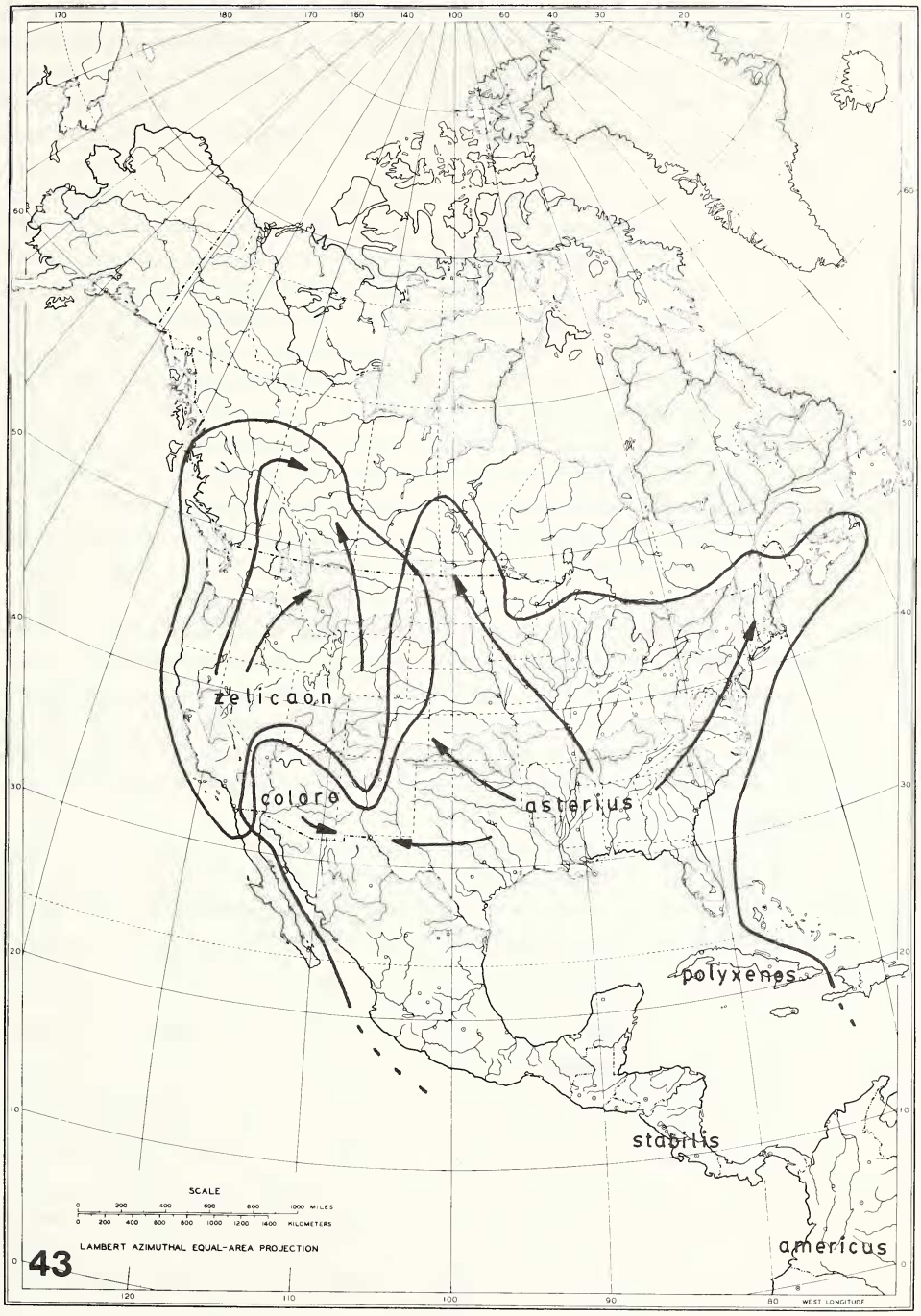


Figure 43. Distribution of *P. zelicaon* and *P. polyxenes*. Arrows show hypothesized Holocene dispersal routes in North America.

The P. machaon lineage.— The *P. machaon* lineage now contains only one species other than *P. machaon* itself. This is *P. hospiton*, which must have become isolated on Sardinia and Corsica very early in the history of the lineage. Rumbacher and Seyer (1979) estimated that this happened during the Mindel glaciation, the second of the four major glacial periods recognized in Europe. The rest of the *P. machaon* lineage occupied most of the Palearctic region, apparently giving little opportunity for populations to develop into anything other than distinct regional races.

The Pleistocene glaciations were probably especially important to acquisition of composite-feeding habits by larvae of *P. machaon* (Figure 40). North America was occupied early in the history of the species group, and so *P. machaon* may have existed for a time in parapatry with the southern species. This kind of replacement may have been similar to that of *P. zelicaon* and *P. polyxenes*, which are presently parapatric over a considerable distance in the western United States. Considering degree of differentiation in the *Artemisia*-feeding subspecies, invasion of western United States by populations with this adaptation must have occurred before the Sangamon Interglacial.

The foodplant shift may have occurred in Beringia, when local populations began to feed on *Artemisia arctica*, a species which is still the main foodplant of Nearctic *P. machaon* in Beringia, and is much more abundant than any umbellifer species in the region. The shift would have been aided by several similarities in secondary plant compounds between plants of the genus *Artemisia* and those belonging to the Umbelliferae (Dethier 1941; Berenbaum, 1983). The plant assemblage of the arctic steppe tundra in Beringia (Matthews, 1982) was probably very similar to that presently occupying the dry, cold climate of northern Afghanistan, the only region in Eurasia in which *P. machaon* has been recorded on *Artemisia*. The later switch of *P. machaon* to *Artemisia dracunculus* in North America may have occurred in Beringia or farther to the south, during a warming trend when Beringian populations came into contact with southern dryland habitats. In any event, the switch to *A. dracunculus* is associated with occupation by *P. machaon* of large regions in sympatry with *P. zelicaon*, *P. indra*, and, in part, *P. polyxenes* (Figures 40, 42 and 43).

A major factor in differentiation of *P. machaon* in North America would have been contact with *P. polyxenes*. Introgression or even more widespread hybridization just after contact with *P. polyxenes* is probably the reason why *P. m. bairdii* acquired the genes for the black morph adult (Figure 39). Support for this suggestion may be derived from the marked similarity between artificial hybrids of *P. machaon* and *P. polyxenes*, and the naturally occurring black morph of *P. m. bairdii*. Though the black morph of *P. machaon* may also be found some distance from the nearest population of *P. p. asterius*, it is restricted to a region where either past contact or allele movement through introgression can account for its occurrence.

During late Wisconsinan time, around 18000 years before present, *P. machaon* must have survived in North America in several different refugia (Figure 41). *P. m. aliaska* would have been restricted to the northernmost refugium, dispersing southward along the Rocky Mountains of northern British Columbia when glacial ice melted. Movements of *P. m. hudsonianus* are postulated with less certainty. The subspecies now ranges to Québec, but is very uncommon west of Saskatchewan. This suggests that it diverged from *P. m. aliaska* before the late Wisconsinan, and occupied the boreal region south of the ice during the last major glaciation (Figure 42).

The stock that *P. m. bairdii* is derived from probably survived in the remnants of desert habitats in the American southwest, and it seems likely that *P. m. oregonius* is derived from a

separate population, suggested by the fact that *P. m. oregonius* has no black form like the one predominant in *P. m. bairdii*. Although most reconstructions of vegetational history show only conifer forest grading into tundra at the edge of the glaciers in the northwestern United States, I suggest that a probable Wisconsinan refugium for *P. m. oregonius* was along the eroding banks of the Columbia River, between Washington and Oregon. Though very close to the ice, the steep north bank of the river must have had a much drier climate than the surrounding region, much like that presently characteristic of the Peace River region. It is even possible that there were dry-tundra adapted *P. machaon* populations along the southern edge of the ice in Washington during the Wisconsinan glaciation, giving rise to *P. m. oregonius* separately from *P. m. bairdii*.

P. m. dodi is even more problematical, possibly surviving on eroding river banks in the drier areas of the northern Great Plains. However, much of the region was covered by conifer forest, and if *P. m. hudsonianus* also survived south of the ice, it would probably have had some contact with *P. m. dodi*, and yet the latter has a distinctively darker wing and body coloration. A more likely alternative is that *P. m. dodi* did not exist as a distinctive population during late Wisconsinan time. The dark adult coloration could have arisen through hybridization of *P. m. oregonius* and *P. m. bairdii* when these two populations contacted each other during the Holocene (Figure 39). A second explanation is introgression from *P. zelicaon* in founding populations of *P. m. dodi*, but since there is no evidence for it in electrophoretic characters, this is less likely.

P. m. pikei probably had a separate origin from the *A. dracunculus*-feeding subspecies which range into the western United States. Although almost all of the butterfly species living with it in the Peace River grasslands are clearly derived from conspecific populations in southern Alberta, (E.M. Pike and F.A.H. Sperling, unpublished), *P. m. pikei* is less like *P. m. dodi* than any other subspecies of *P. machaon* in western Canada. *P. m. pikei* shows a much greater phenetic similarity to populations of *P. m. oregonius* living in southern British Columbia. However, it is unlikely that *P. m. pikei* has been derived from *P. m. oregonius* since evidence available from pollen cores (*e.g.,* Hanson, 1949, 1950, 1955; Valentine *et al.*, 1980; White and Mathewes, 1982) does not suggest that the grassland vegetation of interior British Columbia extended across the Rocky Mountains during the Holocene. Thus it is unlikely that *P. m. oregonius* was able to reach the Peace River area.

I believe it likely that *P. m. pikei* differentiated during the Holocene from *P. m. aliaska*. If larger size and more pointed wings are considered as recent adaptations convergent with other ecologically similar races of *P. machaon* then the greatest morphometric similarity is with *P. m. aliaska*, or perhaps *P. m. hudsonianus*. *P. m. pikei* has an unusual combination of electrophoretic character states, perhaps due to sampling error or genetic drift in the original colonists, but is slightly more similar to *P. m. aliaska* than to any other *P. machaon* subspecies (Table 7). The most westerly populations of *P. m. pikei* presently live about 25 km from the nearest alpine populations of *P. m. aliaska*.

The most likely time of divergence for *P. m. pikei* is between 8000 and 11000 years B.P. The ice-free section of the foothills east of the Rockies had a periglacial climate at about 11,250 B.P., which was dominated by *Artemisia* and grasses (Schweger *et al.*, 1981). However, between 9000 and 6000 B.P. the climate was much hotter and drier than at present, allowing a major expansion of grassland habitats. The relatively rapid shift from dry tundra to hot grassland may have been an important factor in the differentiation of *P. m. pikei* on the Peace River grasslands.

P. zelicaon and hybrids.— *P. zelicaon* represents a lineage similar in age to the *P. machaon* and *P. polyxenes* lineages, and yet shows much less tendency toward the development of geographic races. The reason for this may be that its range has not been fragmented much by Pleistocene glaciations and habitat changes. *P. zelicaon* probably occupied a large proportion of the western United States even during the late Wisconsinan maximum (Figure 41), and its range may have bisected that of the *A. dracunculus*-feeding populations of *P. machaon*

During the post-Wisconsinan climatic amelioration, *P. zelicaon* would have expanded its range into western Canada from two separate directions (Figure 43). One dispersal route was along the foothills and edge of the Great Plains, and brought genes for the black morph to the prairies and southern foothills of Alberta. The other disperal wave occupied all of British Columbia and spread into Alberta through low mountain passes. It colonized the Peace River region and the northern part of central Alberta.

The two-pronged dispersal of *P. zelicaon* into Alberta seems to have effectively isolated a pre-existing population of *P. machaon* in the foothills of central Alberta. Since most remnants of this population presently live in forested areas south of Cadomin, the population probably was not associated with the alpine refugium discussed by Pike (1980). This *P. machaon* population came in direct contact with *P. zelicaon* on all sides and may have had a relatively low population density, much like *P. m. hudsonianus* populations in northern Saskatchewan and Manitoba. A significant number of individuals must have begun to hybridize with those of invading *P. zelicaon* and eventually formed hybrid populations along the ecotone between montane and boreal forest in central Alberta.

In central Alberta, formation of hybrid populations may have occurred gradually during several thousand years. However, the process appears to have stabilized before the region was affected by agricultural disturbances about 100 years ago. I have seen several specimens collected by F.H. Wolley Dod (1901, 1908) around the turn of the century at the "Head of Pine Creek", near Bragg Creek, and these are identical to the hybrid swarm specimens which I have collected in the same area during the last decade.

The Cypress Hills *P. machaon X zelicaon* hybrids are very similar to many of the hybrid specimens from the southern part of the central Alberta hybrid region, and yet do not show any of the more extreme *P. m. hudsonianus*-like characters present in central Alberta. Continuing hybridization with *P. m. dodi* is a possibility in the Cypress Hills, though it would be difficult to demonstrate using the characters employed in this study. However, *P. m. dodi* and *P. zelicaon* appear to hybridize very little in prairie areas of southern Alberta, much like *P. m. oregonius* and *P. zelicaon* in southern British Columbia. Another explanation for the absence of *P. m. hudsonianus*-like specimens may be that the genome of the hybrid swarm is composed of a higher proportion of *P. zelicaon* genes than in central Alberta. Allele distributions in *Pinus contorta* Loudon suggest that the Cypress Hills was a forest refugium during the late Wisconsinan glaciation (Wheeler and Guries, 1982), and so there may have been a *P. machaon* population on the Cypress Hills during this time.

P. polyxenes and hybrids.— *P. p. asterius* has a range approximately as extensive as that of *P. zelicaon* (Figure 43) and shows a similar amount of phenotypic and ecological variation. However, *P. polyxenes* includes several other subspecies and two other species have arisen from the same lineage (Figure 39). The additional *P. polyxenes* subspecies range from the American southwest to northern South America and tend to have a more primitive phenotype expressed in the adults and larvae. They are probably phylogenetically older than the related species in the *P. polyxenes* lineage.

In the *P. polyxenes* lineage is *P. joanae*, which appears to be a taxon with only slight (and dubiously significant) differences from *P. polyxenes*. Also included is *P. brevicauda*, a species restricted to the seashore rim in maritime Canada, which probably survived the late Wisconsinan on the exposed ocean shelves in this region (Figure 41, Matthews, 1979). Adults of both of these species have a wing pattern very similar to *P. p. asterius* and must have achieved reproductive isolation from the latter in the late Pleistocene at the earliest. The gene for the black adult wing morph probably originated in the early Pleistocene, but underwent significant modification during the early history of the *P. polyxenes* lineage, after the divergence of the southern subspecies (Figure 39).

P. p. asterius probably survived the late Wisconsinan in the ecotone between woodland and grassland in the southern part of the eastern and central United States (Figure 41). During post-glacial times this race would have extended its range northward to southern Canada (Figure 43). However, *P. p. asterius* may have had a smaller range and a lower population density before North America was settled by Europeans during the past three centuries (Feeny *et al.*, 1985). It probably reached Nova Scotia only about 60 years ago (Ferguson, 1954), and still seems to be expanding its range in agricultural regions in central Manitoba and Saskatchewan. *P. p. asterius* must have contacted *P. zelicaon* much earlier in the Holocene or even the late Pleistocene, for the black morph on the eastern edge of *P. zelicaon* to have spread several hundred kilometers beyond the range of *P. polyxenes*.

It is doubtful that *P. p. asterius* had any significant amount of contact with *P. m. hudsonianus* during the late Wisconsinan glaciation, even if both survived in refugia within a few hundred kilometers of each other. They are presently allopatric over most of their range, though hybridization has been extensive where they contact each other in central Manitoba. This hybridization shows signs of not yet having reached an equilibrium, since *P. m. hudsonianus* and hybrid forms have become less common in Riding Mountain Park during the past 50 years.

Speciation Mechanisms

Race formation in the *P. machaon* group seems to occur fairly quickly, with ecologically and even phenetically distinctive populations differentiating in a matter of a few thousand years or even a few hundred years under exceptional circumstances. Recent race formation seems to have taken place both at the edge of and in the middle of the range of widespread taxa, when slightly different new larval foodplant resources became available and were opportunistically colonized by individuals from the adjacent population. The most obvious examples include the populations of Californian *P. zelicaon* whose larvae feed on introduced foodplants (Shapiro and Masuda, 1980), and the Peace River race of *P. machaon*

The formation of species seems to have taken much longer than the formation of ecological races, and was probably the result of the adaptation of geographically isolated populations to successively more different habitats. Speciation in the *P. machaon* group probably takes place over hundreds of thousands of years. The low species diversity of the *P. machaon* group in the Palearctic region, despite formation of many geographic races, suggests that speciation can not occur unless there is an extended period of geographic allopatry. However, even if two populations have been separated for enough time to acquire an independent evolutionary identity, hybrid populations may still form between separate species.

The maintenance of separate genetic identity is probably dependent on the degree and kind of ecological differences between two populations when they meet. Genetic mechanisms for

diapause determination are examples of the importance of ecological adaptations in the *P. machaon* group. Hybrids between *P. zelicaon* and *P. machaon* (see phenology section) or *P. polyxenes* (Oliver, 1969) may emerge at a time which is not only different from both of the parental species but is also likely to be inappropriate to the local habitat conditions. Considering the many interrelated factors that are associated with phenology, such as larval foodplant availability, speciation and race formation probably involve substantial reorganization of polygenic balances (*sensu* Carson, 1981).

In the *P. machaon* group, a variety of ecological factors are associated with the coexistence of more than one species in the same geographic region. A difference in larval foodplant is probably the most obvious of these factors. The greatest local species diversity anywhere within the range of the *P. machaon* group occurs in Arizona and southeastern California. Here larvae of *P. indra* feed on umbellifers, those of *P. m. bairdii* feed on composites, and *P. p. coloro* larvae have switched back to a more ancestral foodplant group for *Papilio*, the Rutaceae. However, larval resource partitioning does not necessarily imply competition for these resources (as suggested, for example, by Miller and Brown, 1983). Though Emmel and Emmel (1969) and Blau (1980) have indicated that larval resources may sometimes limit population sizes in the *P. machaon* group, direct larval resource competition between species has not yet been demonstrated.

Natural Hybridization

Hybridization between closely related species is a well known event in both plants and animals. The phenomenon is, by definition, in conflict with the biological species concept. Most animal taxonomists deal with this by describing hybridization as interspecific only if hybrids are rare in comparison with the parental forms. However, for some species pairs, hybridization is relatively common and yet the parental species maintain their integrity. The species in such a taxonomically difficult group are termed semispecies by some authors, while the group itself may be termed a superspecies (Mayr, 1963). The term semispecies is appropriate for the species in the *P. machaon* group, since these are more reproductively isolated than geographic subspecies and yet hybridize relatively freely in comparison to most other species.

Under some conditions, hybrids are especially common. Such conditions include habitat disturbance, of which the most common source is the clearing of forests by man. However, increased rates of hybridization generally take place in very restricted geographic areas. If hybridization occurs along a narrow line of contact between parapatric species, then such an area is referred to as a hybrid zone. Hybrid individuals may comprise small or large proportions of populations in hybrid zones, and may also be present in varying frequencies within larger areas of overlap between parental species. The species of the *P. machaon* group in western Canada show a low but persistent rate of hybridization in most areas where they come into contact, and in some areas have formed populations in which hybrid individuals are numerically dominant (Figure 44).

Hybrid zones.— The zone of hybridization between two species may vary in width from a few hundred meters to more than a hundred kilometers, but is much narrower than the total range of the parental species (Barton and Hewitt, 1981 and 1985). Most hybrid zones are much longer than they are wide, and some span an entire continent. In the *P. machaon* group, the best examples of hybrid zones are along the periphery of the range of *P. polyxenes* In the American West this species replaces *P. zelicaon* along major ecotones. It involves a replacement over a few dozen kilometers of *P. polyxenes* by *P. zelicaon* in wetter habitats and

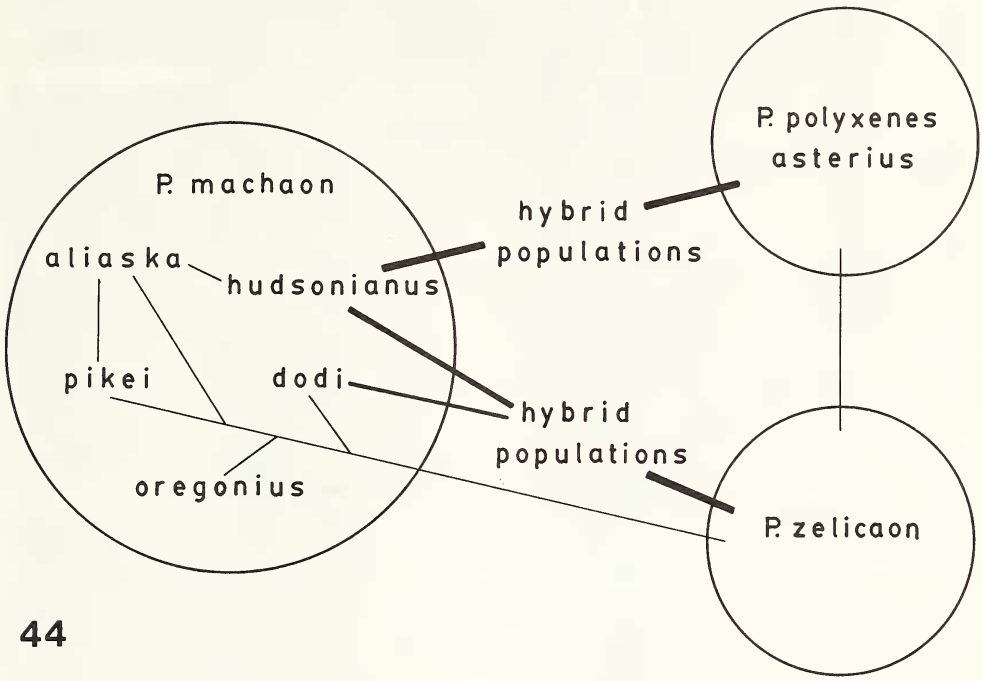


Figure 44. Hybridization of *P. machaon* group species in western Canada during recent time. Circles indicate species. Relative thickness of lines is proportional to rates of hybridization.

higher altitudes. A similar pattern also applies to the transition from *P. polyxenes* to *P. m. hudsonianus* in cooler habitats in Manitoba, though the width of the real zone of intergradation between the two species remains uncertain. In both comparisons, the zones are relatively wide compared to other animals, probably because of the good dispersal powers of *Papilio* butterflies (Shields, 1967).

The pattern of variation across a hybrid zone may not be a simple cline, but rather a mosaic of populations (Harrison, 1986). This is clearly true of the *P. machaon* group, and appears to be closely associated with an interdigitation of habitats across major ecotones.

The influence of environmental factors on the location of major hybrid populations is supported by the coincidence of the *P. zelicaon* X *machaon* populations in central Alberta with ecological boundaries and hybrid zones in other species. For example, the southern limit of the hybrid populations in southern Alberta occurs very near to the southernmost limit of many boreal elements. Black spruce (*Picea mariana* [Mill.]BSP) is found in Alberta only as far south as Bragg Creek, while three butterfly taxa characteristic of spruce bogs are also found south to near Bragg Creek. These include *Colias gigantea gigantea* Strecker, *Oeneis jutta chermocki* Wyatt, and *Erebia disa* (Thunberg). The northern limit of the *P. machaon X zelicaon* hybrid populations in central Alberta also coincides generally with the location of several hybrid zones in unrelated taxa. An example is the hybrid zone between *Pinus contorta* and *P. banksiama* Lamb., (with a corresponding contact zone between the pine-feeding butterflies *Incisalia*

eryphon (Boisduval) and *I. niphon* (Huebner), - Reist, 1979). I am not aware of any animal taxa which form self reproducing hybrid populations within Alberta. However, in plants there is a wide ranging hybrid swarm in the genus *Betula*, which has a distribution very similar to that of the *P. machaon X zelicaon* swarms in central Alberta (Dugle, 1966).

Some hybrid zones appear to have moved a few dozen kilometers within the last century (*e.g.,* McDonnell *et al.*, 1978). However, such movement is uncommon, and most hybrid zones appear to remain relatively stationary over long periods of time. In fact, many hybrid zones probably become trapped in regions of low density, such as habitat clines and natural barriers (Barton, 1979). They may also become narrower, especially if there is strong selection against hybrids, or they may widen and eventually result in the merging of the two parental species. In the *P. machaon* group, evidence suggests that some hybrid zones may presently be undergoing change, probably because they are very recent, having been influenced by human settlement patterns. The range expansion of *P. polyxenes* into Nova Scotia and Manitoba is probably related to deforestation by man, and so it seems likely that any interaction of this species with *P. brevicauda*, in the east, and *P. m. hudsonianus*, in the west, is less than a century old. The decreasing proportion of *P. machaon* in Riding Mountain Park in Manitoba is thus probably a result of genetic swamping by recently arrived *P. polyxenes* in agricultural areas.

Most hybrid zones for both plants and animals, appear to be the result of secondary contact between formerly allopatric species (*e.g.,* Remington, 1968b; Barton and Hewitt, 1985). However, a few hybrid zones may be the result of *in situ* differentiation on either end of a sharp environmental gradient (Endler, 1977). Most authors do not believe that they can distinguish between these two situations, though Thorpe (1984) states that a phylogenetic analysis at the population level makes such distinctions possible. In the *P. machaon* group it seems most likely to me that most, if not all, of the hybrid zones can most parsimoniously be explained as the result of post-Pleistocene range expansions. However, if *P. m. hudsonianus* spent the late Wisconsinan south of the continental ice sheet, then there may have been a pattern of contact between *P. m. hudsonianus* and *P. p. asterius* which was similar to the present one. The contact zone between *P. zelicaon* and *P. m. aliaska* is certainly the result of secondary contact.

Hybrid zones which show substantial gene flow are generally no longer considered to represent interspecific hybridization, but rather zones of contact between different races of a single species. Examples include subspecies within both *P. machaon* and *P. polyxenes* in the western United States. However, the degree of gene flow has only been indirectly interpreted from morphological and ecological character gradients and could bear rechecking against enzyme allele distributions. In particular, it should be interesting to compare the rate of gene flow between *P. p. asterius* and *P. p. coloro* in New Mexico with that between *P. p. coloro* and *P. zelicaon* in southern California. Enzyme data for western Canada show a significant interruption in gene flow between *P. machaon* and *P. zelicaon* in most regions in Alberta and British Columbia.

Though both electrophoretic and morphometric character distributions can indicate gene flow across hybrid zones, there may be some differences between these character types. This is true of the *P. machaon* group hybrid populations in both central Alberta and Manitoba, where electrophoretic character combinations showed greater intermediacy than did morphometric characters. Harrison (1986) reported a similar situation in a hybrid zone in crickets, and suggested that there were fewer barriers to the introgression of allozyme alleles than morphometric characters. A possible reason for this is that the inheritance of morphometric characters is more canalized, with a greater degree of linkage between genes and a resultingly

greater resistance to the movement of such traits.

The evolutionary importance of interspecific hybridization is not clear, though various authors have suggested that gene introgression provides an important source of allelic variation for action of natural selection. However, most studies of gene flow in hybrid zones show only limited intrusions of alleles into neighboring species (Barton and Hewitt, 1985). The black morph in the *P. machaon* group generally follows this pattern as well, though it has moved several hundred kilometers into the range of *P. zelicaon* and has displaced the yellow allele in the southern part of the range of *P. machaon*.

The selective advantage of alleles which produce the black adult morph is unknown. Since many populations are polymorphic with respect to this allele, it is probably not important as a visual mechanism for mate recognition, as Hafernik (1982) reported for an analogous wing pattern in *Junonia* (Nymphalidae). It may give hilltopping males an advantage in maintaining a position at the very peak of hills (Scott, 1983 and personal observations). However, Miller (1977) suggested that the allele is lethal when homozygous and in combination with the *P. zelicaon* genome. Perhaps the distribution of the allele is the result of an equilibrium between positive and negative selection, much as hybrid zones themselves may be a balanced conflict between genes that widen zones by reducing incompatibilities and genes that narrow zones by producing reproductive isolation (Barton and Hewitt, 1981).

Hybrid populations.— Some populations in interspecific hybrid zones are characterized by negative or neutral selection on hybrid individuals in the contact zone. However, hybrid populations are characterized by positive selection for interspecific hybrids in restricted areas, even though the parental species retain their integrity over most of their area of contact. Hybrid populations are composed predominantly of hybrid forms, and variation within most such populations spans the full range of phenotypes between the parental forms. In a fully integrated hybrid population, individuals phenotypically similar to parental forms simply represent the phenotypic extremes within the population.

Hybrid populations are reasonably common in plants, with many referred to as hybrid swarms, but are very unusual in animals (Mayr, 1963; Grant, 1971). Most animal examples are of birds, amphibians and fish (Moore, 1977), and the studies of Sibley (1954) on towhees and those of Blair (1941) and others on toads are still among the best documented. Examples of hybrid populations not clearly associated with narrow zones are much less common in insects.

The present study provides a clear example of hybrid populations between broadly sympatric species. In the *P. machaon* group the best examples of hybrid swarms are the *P. machaon X zelicaon* populations in central Alberta, particularly the one at Bragg Creek. The Bragg Creek population is composed of a highly varied but unimodal population made up almost completely of hybrid forms, and probably has no significant internal impediment to gene flow. The intermediate nature of the central Alberta populations is indicated by both the morphometric and electrophoretic character distributions.

Many hybrid populations are associated with environmental disturbance of some sort, resulting in a kind of hybrid habitat, in which forms intermediate between the parental species can flourish. Habitat disturbance by man in recent times, has provided several opportunities to observe the formation of new hybrid swarms over a period of only a few decades (*e.g.*, Gillespie, 1985). An interesting aspect of some hybrid populations is that they separate again into parental forms within about 20 years (Jones, 1973; Corbin *et al.*, 1979). Considering the ephemerality and dependence on habitat disturbance of many hybrid swarms, the examples of the *P. machaon* group from central Alberta are fairly unusual. They occur in areas with

relatively little or no habitat disturbance, especially compared to the regions dominated by agriculture where *P. machaon* and *P. zelicaon* coexist with only a small amount of hybridization. As well, material collected around 1900 suggests that the hybrid populations were already in existence when central Alberta was first being settled.

Although artificial hybrids within the *P. machaon* group have invariably been obtained between individuals from geographically distant populations, and many showed substantial infertility even when they were from interspecific populations clearly connected by character clines, some backcrosses to either of the parental species have produced viable adults (Clarke and , 1953; Ae, 1966; Clarke *et al.*, 1977). In a few crosses, adults have even been obtained from an F_2 hybrid cross of *P. polyxenes* and *P. machaon* (Ae, 1964). These experiments indicate that introgression and the formation of hybrid swarms are at least possible, though unlikely.

However, at least part of the inviability of hybrids is due to environmental adaptations, such as diapause characteristics (Oliver, 1969). Since the three species in western Canada are very flexible in their adaptation to different environmental factors, it is reasonable to expect that species coming together in a particular region tend to be more similar than would populations from more distant regions. Unless some fundamentally different ecological adaptation has occurred, adjacent populations seem likely to meet and hybridize on a continuing basis, until reproductive isolation occurs. Thus the reason for formation of *P. machaon X zelicaon* hybrid swarms in central Alberta is probably related to similarities in the habitat preferences of local races before contact occurred through range expansions. The two species coexist where *P. machaon* larvae feed on *Artemisia* and where adult contact is reduced through the occupation of different habitats. Where *P. machaon* occupies a habitat more similar to that of *P. zelicaon*, as does *P. m. hudsonianus*, the two species have tended to merge, with the hybrid populations feeding on plesiotypically palatable umbellifers. This situation is similar to that described by Mayr (1963) for *Passer domesticus* (Linneaus) and *P. hispaniolensis* Temminck in Europe.

Many plants form hybrid swarms, and the frequency with which such events occur may be related to ecological characteristics of particular taxa (Raven, 1976). Some plant species tend to maximize the saturation density (K) of their populations and are separated by ecological and other extrinsic factors, but have only slightly developed internal barriers to hybridization. They hybridize with related species to form new recombinants, which allow populations to adapt to changing environments. On the other hand, species whose populations maximize their rate of increase (r), such as annual herbs, tend to hybridize much less frequently with each other. Since they are characterized by rapid dipersal and growth in new areas, as well as a high commitment of basic resources to reproduction, barriers to hybridization are much more important to these species. This correspondence between maximization of saturation density and tendency toward hybridization in plants does not seem to apply to the *P. machaon* group. These butterflies would, if anything, be considered as maximizing their rate of increase, since they feed in the larval stage on successional plants and are dependent on rapid colonization and foodplant exploitation. However, it would be interesting to investigate the *P. machaon* group to determine if introgression enhances adaptation to new ecological conditions.

The phylogenetic significance of hybrid swarm formation is uncertain. It may be rare enough in animals so that it has had little influence on evolutionary patterns. However, it may be that such breakdowns in reproductive barriers contribute to the formation of new populations under conditions in which one of the parental species would have been eliminated by habitat destruction. In this way part of the threatened gene pool is saved, albeit in a greatly

altered combination. Formation of hybrid populations may also cause a major disorganization of the polygenic balances of the parental species, leading eventually to speciation through a major new balanced genetic system (Carson, 1981).

New species that may have arisen from interspecific hybrid swarms would be impossible to detect by morphological features if the hybridization occurred between a pair of sibling species. On the other hand, if the new species is the product of hybridization between species A and C, and there exists a species B which is more closely related to A than C is, then the hybrid origin of the new species would be indicated by its discordant character distribution. Unfortunately, as Mayr (1963) pointed out, such a character distribution could also easily be due to the character convergences and parallelisms which one would expect in closely related species with a very similar basic gene pool. For these reasons, the number of animal taxa which have had a hybrid origin has almost certainly been underestimated, and will continue to remain so until there has been ample opportunity to support or reject present taxonomic assignments with independent character suites, such as enzyme alleles or mitochondrial DNA.

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Appendices: Tables 12-14

Table 12. PCA and DFA loadings for morphometric characters.

Characters	No. of states	Prescaling factor	Morph. char. alone PC1	PC2	PC3	Morph. + E4 char. PC1	PC2	PC3	Morph. char. Discr. axis 1	Discr. axis 2
1. DHW anal yellow exent	4	0.67	-.088	.127	.277	-.084	.028	.086	-.956	.450
2. DHW eyespot pupil shape	4	0.67	.281	.196	.102	.267	-.058	-.039	2.63	.273
3. DHW anal red/blue separ.	3	1.00	.376	.273	.800	.273	.166	.224	.146	.554
4. Tegula color	3	1.00	.074	-.332	.116	.033	.196	-.154	---	--.
5. VFW discal yellow	4	0.67	.515	.064	-.287	.373	.201	.209	.396	.437
6. VFW apical yellow smudge	3	1.00	.088	-.410	.094	.036	.223	-.139	-2.79	1.63
7. VHW postmedian orange	8	0.30	.145	-.286	.164	.089	.199	-.064	.669	-1.10
8. Metathoracic yellow	3	1.00	.367	-.177	-.153	.251	.234	.052	.286	-.459
9. Abdominal ventral line	9	0.25	.562	.152	-.295	.409	.196	.264	-.062	.352
10. Abdominal lateral line	3	1.00	.125	-.488	.099	.059	.267	-.179	.138	1.15
11. Abdominal upper line	9	0.25	-.080	.462	-.141	-.028	-.243	.164	-1.18	3.57
% Variance :			54.6	69.8	78.2	32.2	44.4	52.4	89.9	100.

Table 13. PCA loadings for electrophoretic characters.

		E4 char. alone			E4 + morph. char.		
	RF	PC1	PC2	PC3	PC1	PC2	PC3
1. Est4 -A	.48	.513	.153	-.029	-.333	.364	.057
2. Est4 -B	.54	-.513	-.153	.029	.333	-.364	-.057
3. Est5 -I	.57	.003	.001	.003	-.001	.002	.004
4. Est5 -A	.64	.194	-.083	.049	-.134	.028	.202
5. Est5 -B	.65	.001	.006	-.009	-.001	.005	-.011
6. Est5 -C	.71	-.188	.080	-.041	.126	-.035	-.197
7. Est5 -D	.75	-.010	-.004	-.003	.010	.000	.002
8. IDH -A	.16	.015	.006	.039	-.008	.014	.030
9. IDH -B	.18	-.178	.109	-.678	.082	-.143	-.490
10. IDH -C	.20	.012	-.010	.041	-.003	.014	.039
11. IDH -D	.22	.148	-.108	.595	-.069	.114	.421
12. IDH -E	.24	.002	.003	.003	-.002	.001	.000
13. G-6-PD -E	.16	-.006	-.006	-.002	.004	-.006	.001
14. G-6-PD -A	.18	-.003	-.025	-.046	-.005	-.019	-.028
15. G-6-PD -B	.20	-.395	-.016	.205	.264	-.232	.001
16. G-6-PD -I	.22	.027	.026	.023	-.010	.024	.021
17. G-6-PD -K	.24	-.008	.191	-.017	.036	.168	-.146
18. G-6-PD -C	.26	.387	-.171	-.206	-.293	.053	.108
19. G-6-PD -D	.30	.006	.000	.043	.002	.012	.044
20. ME -J	.475	.001	.017	-.001	.001	.013	-.013
21. ME -I	.500	.022	.055	-.007	-.016	.026	-.029
22. ME -A	.525	.110	.076	-.056	-.087	.027	-.028
23. ME -B	.550	-.118	-.188	.045	.082	-.086	.073
24. ME -K	.575	-.005	.017	.007	.006	.009	-.006
25. ME -C	.600	-.010	.015	.013	.012	.005	.007
26. ME -D	.625	.000	.008	-.002	.001	.006	-.005
27. ODH -A	.17	-.020	-.020	.001	.014	-.013	.001
28. ODH -B	.21	.034	.084	.061	-.006	.071	.037
29. ODH -C	.25	-.014	-.064	-.062	-.008	-.058	-.038
30. MDH -I	.16	-.004	.008	.001	.003	-.000	-.004
31. MDH -A	.18	.002	-.013	.014	-.001	-.001	.013
32. MDH -B	.22	.001	.001	-.024	-.004	-.006	-.014
33. MDH -C	.26	.002	.004	.008	.001	.007	.004
34. aGPD -A	.29	-.002	-.001	.000	.001	-.001	.000
35. aGPD -B	.32	.001	.000	.003	.000	.004	.003
36. aGPD -C	.35	.000	.001	-.003	-.002	-.002	-.003
37. Prot1 -A	.21	-.065	.119	.179	.085	.087	.084
38. Prot1 -B	.26	.065	-.119	-.179	-.085	-.087	-.084
39. Prot2 -I	.300	.002	.006	.004	-.002	.000	-.001
40. Prot2 -A	.315	-.042	.613	.067	.073	.278	-.275
41. Prot2 -B	.330	.037	-.623	-.070	-.070	-.282	.275
42. Prot2 -C	.345	.003	.004	-.001	-.000	.004	.001
% Variance :		31.0	43.2	53.0	32.2	44.4	52.4

Table 14. Larval foodplant records.

Only wild collected larvae and confirmed ovipositions under natural conditions are included. Entries are arranged by taxon and region. All entries from a particular locality are grouped together, even though entries from major hybrid zones produced a variety of adults. Uncredited entries refer to personal obsevations or collections. Abbreviations: AB = Alberta, BC = British Columbia, MB = Manitoba, SK = Saskatchewan, NWT = Northwest Territories.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. aliaska				
Pink Mt.(alpine), BC	*Artemisia arctica*	6 July 1981	1 egg	not emg.
Pink Mt.(alpine), BC	*Artemisia arctica*	17 Aug. 1982	4-3rd, 3-4th,16-5th	1m, 2f
Eagle Summit, Alaska	*Artemisia arctica*	197?	1 egg, K.Phillip (pers.comm. 1983)	not reared
Dawson, Yukon	*Artemisia arctica*	1949	ovip. obs. by P. Bruggeman (Freeman, 1949)	
Richardson Mts., Yukon	*Artemisia arctica*	June 1981	ovip. obs. by J. Troubridge -*in litt.* 1981.	not reared
near Aklavik, NWT	*Petasites palmatus* var. *frigidus*	1931	larvae observed by O. Bryant (Leussler and Bryant, 1935)	
Arctic Red River, NWT	"small low-growing carroty plant" (?*A. arctica*)	late June 1955	oviposition observed by C. Wyatt (1957)	
P. m. hudsonianus				
Jan Lake, SK	?*Sanicula marilandica*	June 1972	ovip. obs. by G. Anweiler (Hooper, 1973),	not reared
Torch Lake, SK	*Petasites palmatus*	August 1976	1-5th, color photo by G. Anweiler	not reared
P. m. oregonius				
Penticton area, BC	*Artemisia dracunculus*	20 August 1980	6-1st,10-2nd,7-3rd,14-4th,15-5th	1m
Penticton area, BC	*A. dracunculus*	1 July 1984	1-3rd, 1-4th	not reared
Macalister-Soda Cr., BC	*A. dracunculus*	18 August 1982	1-1st,1-3rd,2-4th,16-5th,1 pupa	2m, 2f
Savona, BC	*A. dracunculus*	19 August 1982	1-2nd, 2-5th	2f
Kamloops, BC	*A. dracunculus*	26,27 Aug. 1983	1-e, 2-4th, 15-4th, 56-5th	25m, 23f
Grant Co.,Washington	*A. dracunculus*	1 July 1983	"ova & larvae" -Lepidopterists' News (Season Summary 1983)	
Deschutes Park, Oregon	*A. dracunculus*	26 July 1980	14-e,15-1st,25-2nd,12-3rd,6-4th,5-5th	no emg.
Biggs, Oregon	*A. dracunculus*	26 July 1980	1-3rd, 1-4th, 6-5th	1f

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. pikei				
12km ne Hudson Hope, BC	*Artemisia dracunculus*	12 July 1984	2-e, 3-1st	no emg.
12km ne Hudson Hope, BC	*A. dracunculus*	20 August 1984	9-4th, 64-5th	22m, 20f
Attachie, BC	*A. dracunculus*	9 July 1981	2-e,13-1st & 2nd,1-3rd, 1-4th	1m
Attachie, BC	*A. dracunculus*	9 August 1981	11-4th, 41-5th	9m, 4f
Taylor, BC	*A. dracunculus*	18 August 1980	2-5th	1f
Taylor, BC	*A. dracunculus*	8 July 1982	2-1st, 1-2nd, 1-3rd, 1-4th	1m
8 km e. Ft.St.John, BC	*A. dracunculus*	18 August 1980	1-5th	no emg.
Clayhurst Fy., BC	*A. dracunculus*	17 August 1980	1-4th, 59-5th	3m, 5f
Clayhurst Fy., BC	*A. dracunculus*	9 August 1981	3-4th, 46-5th	3m, 2f
Clayhurst Ferry, BC	*A. dracunculus*	16 August 1982	2-4th, 42-5th	12m, 6f
18 mi w Fairview, AB	*A. dracunculus*	21 August 1980	1-5th E.M. Pike -*in litt.*	1980 emg.?
Dunvegan, AB	*A. dracunculus*	13,15,17 Aug.80	4-4th, 24-5th E.M. Pike -*in litt.*	1980 emg.?
Dunvegan, AB	*A. dracunculus*	16 August 1980	6-4th, 32-5th	3m, 3f
Dunvegan, AB	*A. dracunculus*	8 August 1981	7-4th, 15-5th	no emg.
Dunvegan, AB	*A. dracunculus*	15 August 1982	1-4th, 4-5th	1f
Dunvegan, AB	*A. dracunculus*	8 July 1984	1-e, 1-1st (G.J. Hilchie, leg)	no emg.
10 mi s.w. Fairview, AB	*A. dracunculus*	19,28 Aug.& 1 Sept.80	10-5th E.M. Pike -*in litt.*	1980 emg.?
10 mi s.w. Fairview, AB	*A. dracunculus*	15 August 1982	6-5th	no emg.
Camp I., s. Whitelaw,AB	*A. dracunculus*	15 August 1980	1-4th	1m
Shaftesbury Ferry, AB	*A. dracunculus*	15 August 1980	2-5th	1f
Peace River (town), AB	*A. dracunculus*	14 August 1980	4-4th, 56-5th	2m, 1f
Peace River (town), AB	*A. dracunculus*	8 August 1981	1-4th, 3-5th	1f
Peace River (town), AB	*A. dracunculus*	24 July 1983	1-2nd	no emg.
Peace River (town), AB	*A. dracunculus*	18 August 1984	11-5th	2m, 1f
12 mi e. North Star, AB	*A. dracunculus*	11 August 1981	5-5th	no emg.
Kleskun Hills, AB	*A. dracunculus*	12 August 1981	1-5th	1f

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. dodi				
Nevis Junction, AB	*Artemisia dracunculus*	19 August 1981	5-5th	1m
Nevis Junction, AB	*A. dracunculus*	3 Sept. 1982	2-3rd, 2-4th, 17-5th	3m, 3f
Nevis Junction, AB	*A. dracunculus*	8 Sept. 1983	2-5th	no emg.
Tolman Bridge, AB	*A. dracunculus*	30 July 1981	4-5th	2m, 1f
Tolman Bridge, AB	*A. dracunculus*	3 Sept. 1982	1-3rd, 4-4th, 20-5th	5m
Morrin Bridge, AB	*A. dracunculus*	2nd wk. July 80	c.50-1st & 2nd J. Troubridge -*in litt.* 1980	emg.?
Morrin Bridge, AB	*A. dracunculus*	10 August 1980	2-2nd, 8-5th	2f
Bleriot Ferry, AB	*A. dracunculus*	2nd wk. July 80	c.50-1st & 2nd J. Troubridge -*in litt.* 1980	emg.?
Bleriot Ferry, AB	*A. dracunculus*	10 August 1980	2-4th, 14-5th	no emg.
Bleriot Ferry, AB	*A. dracunculus*	22 July 1981	2 larvae -4th or 5th	no emg.
Bleriot Ferry, AB	*A. dracunculus*	20 July 1982	E.M. Pike, pers. comm.	emg.?
Bleriot Ferry, AB	*A. dracunculus*	20 July 1982	1-2nd E.M. Pike, pers. comm.	emg.?
Nacmine, AB	*A. dracunculus*	2nd wk July 80	c.100-1st & 2nd. J. Troubridge -*in litt.* 1980	emg.?
Nacmine, AB	*A. dracunculus*	10 August 1980	2-2nd, 1-3rd, 3-4th, 12-5th	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	c.11 Aug. 1980	21-4th & 5th E.M. Pike, pers. comm.	emg.?
Nacmine area, AB	*A. dracunculus*	22 July 1981	40 larvae, mostly 4th & 5th	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	19 August 1981	5-5th	emg. counted w. Drumheller
Nacmine area(+ Bleriot)	*A. dracunculus*	19 July 1982	2-2nd(Bler.); 1-3rd, 4-5th(Nac.)	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	8 August 1982	3-4th, 8-5th	emg. counted w. Drumheller
Hwy 575, w. Nacmine,AB	*A. dracunculus*	22 July 1981	5 larvae, ? instars, 1 pupa	no emg.
Drumheller, AB	*A. dracunculus*	10 August 1980	2-2nd, 1-3rd, 3-4th, 12-5th	2m, 3f
Drumheller, AB	*A. dracunculus*	22 July 1981	15 larvae, mostly 4th & 5th	6f
Drumheller, AB	*A. dracunculus*	19 July 1982	3-1st, 3-2nd, 2-3rd, 6-5th	4m, 5f
Drumheller, AB	*A. dracunculus*	8 August 1982	2-4th, 17-5th	1m, 2f
Drumheller area, AB	*A. dracunculus*	20 July 1982	1-4th, 7-5th E.M. Pike, pers. comm.	emg.?
Drumheller, AB	*A. dracunculus*	3 Sept. 1982	1-4th, 4-5th	no emg.
East Coulee, AB	*A. dracunculus*	2nd wk July 80	250 larvae, mostly 1st & 2nd J. Troubridge -*in litt.* 1980	
East Coulee, AB	*A. dracunculus*	10 August 1980	7-1st, 5-2nd, 8-3rd, 8-4th, 7-5th	no emg.
East Coulee, AB	*A. dracunculus*	22 July 1981	3-larvae, 4th or 5th	no emg.
East Coulee, AB	*A. dracunculus*	19 August 1981	3-4th, 1-5th	
East Coulee, AB	*A. dracunculus*	19 August 1981	3-4th, 1-5th	no emg.
Dorothy, AB	*A. dracunculus*	2nd wk July 80	48 larvae, mostly 1st & 2nd J. Troubridge -*in litt.* 1980	
Dorothy, AB	*A. dracunculus*	10 August 1980	1-e, 1-1st, 1-2nd, 3-3rd, 1-4th, 3-5th	2m, 1f
Dorothy, AB	*A. dracunculus*	19 July 1982	5-2nd, 1-3rd, 2-5th	1f
Dorothy, AB	*A. dracunculus*	8 August 1982	1-4th	no emg.

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained		
P. m. dodi - continued						
Outlook, SK	*A. dracunculus*	9 Sept. 1982	1-2nd, 1-3rd, 1-4th, 10-5th	6m, 1f		
Outlook, SK	*A. dracunculus*	28 May 1983	ovip. observed	not reared		
Calgary, AB	*A. dracunculus*	30 August 1983	2-4th	no emg.		
Spring Coulee, AB	*A. dracunculus*	29 August 1983	3-4th, 4-5th	4f		
Taber Prov. Park, AB	*A. dracunculus*	10 August 1980	1-1st	E.M. Pike, pers. comm.		emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	7 August 1980	50 larvae, 2nd to 5th	E.M. Pike, pers. comm.		emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	9 August 1980	40 larvae, 2nd to 5th	E.M. Pike, pers. comm.		emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	26 August 1980	13-4th, 37-5th	7m, 17f		
8 mi. s. Vauxhall, AB	*A. dracunculus*	29 July 1981	c.100 larvae, mostly 1st & 2nd	no emg.		
8 mi. s. Vauxhall, AB	*A. dracunculus*	19 August 1981	c.70 larvae, mostly 4th & 5th	17m, 10f		
8 mi. s. Vauxhall, AB	*A. dracunculus*	6 July 1982	30 larvae, mostly 5th	E.M. Pike, pers. comm.		4m, 3f
8 mi. s. Vauxhall, AB	*A. dracunculus*	8 July 1982	10 larvae, 4th or 5th	E.M. Pike, pers. comm.		emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	29 August 1983	1-2nd, 1-3rd, 7-4th, 13-5th	6m, 3f		
P. m. bairdii						
Canyonlands NP, Utah (Needles District)	*Artemisia dracunculus*	20 May 1985	2-3rd	not reared		

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. zelicaon				
southern & interior BC				
Saanich, BC	*Lomatium nudicale*	1957	G.A. Hardy-leg, specm. in BCPM	1f + 1?m
Francis Peak, BC	*Oenanthe sarmentosa*	8 August 1962	G.A. Hardy-leg, specm. in BCPM	1f
Ucluelet, BC	*Heracleum lanatum*	May & July	2nds to 5ths both months	C. Guppy -*in litt.* 1982
Thetis Island, BC	"garden parsley"	"often"	?instars	R. Guppy (1970)
Abbotsford, BC	*Angelica lucida*	?date	?instars "a major foodplant" -H. Kimmich *in litt.* 1982	
Abbotsford, BC	*Sium suave*	end of Aug. 82	mostly 5ths Kimmich *in litt.* 1982	in FAHS colln: 3m,7f
Abbotsford, BC	*Angelica genuflexa*	end of Aug. 82	mostly 5ths Kimmich *in litt.* 1982	included above
Abbotsford, BC	*O. sarmentosa*	c. 10 Aug. 1984	?instars Kimmich *in litt.* 1984	in FAHS colln: 7m,9f
Abbotsford, BC	*Cicuta occidentalis*	c.10 Aug. 1984	?instars Kimmich *in litt.* 1984	included above
Matsqui, BC	*Sium suave*	July & August	all instars Kimmich *in litt.* 1982	?emg.
Manning Park, BC	*Osmorhiza chilensis*	? date	?instars Kimmich *in litt.* 1982	?emg.
Kootenay Skyway Smt.,BC	*Heracleum lanatum*	20 August 1982	1-3rd	1f
5 km s Enderby, BC	*Heracleum lanatum*	30 June 1984	6-2nd, 2-3rd	incl. w. next entry
5 km s Enderby, BC	*Heracleum lanatum*	2 July 1984	3-2nd, 7-3rd, 1-4th, 7-5th	4m, 1f
11 km w Revelstoke, BC	*Heracleum lanatum*	30 June 1984	1-1st, 4-2nd	3m
Rogers, BC (Glacier NP)	*Heracleum lanatum*	30 June 1984	1-1st, 2-2nd	no emg.
Tete Jaune Cache, BC	*Heracleum lanatum*	26 August 1983	1-5th	no emg.
Barkerville, BC	*Heracleum lanatum*	August	?instar N. Criddle-leg, McDunnough (1927)	1f
Macleod Lake,n PrGeo,BC	*Zizia aptera*	? date	?instars H. Kimmich *in litt.* 1982	?emg.
Bear Lk,n.Prince Geo.BC	*Heracleum lanatum*	18 August 1982	1-5th	1-5th
Peace River region				
Pink Mt.(valley), BC	*Heracleum lanatum*	16 & 17 Aug. 82	5-4th, 3-5th	no emg.
Pink Mt.(valley), BC	*Heracleum lanatum*	19 August 1984	1-3rd, 1-5th	no emg.
10km ne Hudson Hope, BC	*Heracleum lanatum*	12 July 1984	5-1st, 2-2nd, 3-3rd, 1-4th	3m
15 km w Ft.St. John, BC	*Heracleum lanatum*	12 July 1984	6-1st,9-2nd,4-3rd,2-4th,2-5th	no emg.
Cecil Lake, BC	*Heracleum lanatum*	9 July 1984	4-1st, 2-2nd E.M. Pike -pers. comm.	?emg.
30 mi w Dawson Creek,BC	*Zizia aptera*	2 July 1982	1-2nd, 1-3rd, 1-4th	1m, 1f
30 mi w Dawson Creek,BC	*Zizia aptera*	10 July 1984	2-1st	no emg.
40 km w Dawson Creek,BC	*Heracleum lanatum*	10 July 1984	2-1st, 6-2nd, 1-3rd	no emg.
18 km w Dawson Creek,BC	*Heracleum lanatum*	10 July 1984	17-1st, 6-2nd, 3-3rd, 3-5th	1m
w. Chetwynd, BC	*Heracleum lanatum*	18 August 1982	1-5th	no emg.
Thunder Mt., BC	*Heracleum lanatum* & *Angelica genuflexa*	9 July 1982	7-1st, 9-2nd, 4-3rd	1m

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. zelicaon - continued				
14 mi. w. Elmworth, AB	*Heracleum lanatum*	9 July 1982	2-1st, 4-2nd	not reared
3.5 km nw Wembley, AB	*Heracleum lanatum*	10 July 1984	4-1st, 5-2nd, 3-3rd, 2-4th	1m, 3f
3.0 km nw Wembley, AB	*Sium suave*	10 July 1984	1-e, 4-1st	1m
2 km e Woking, AB	*Heracleum lanatum*	8 July 1984	1-1st, 5-2nd, 2-3rd	1f
2 km e Woking, AB	*Zizia aptera*	8 July 1984	2-1st	no emg.
2 km w Debolt, AB	*Sium suave*	12 July 1984	1-5th	1f
13 mi. w Valleyview,AB	*Heracleum lanatum*	9 July 1982	5-2nd, 8-3rd, 18-4th, 22-5th	2m, 1f
13 mi. w Valleyviw, AB	*Heracleum lanatum*	12 July 1984	8-1st,17-2nd,8-3rd,4-4th,6-5th	no emg.
15 mi e High Prairie,AB	*Heracleum lanatum*	27 July 1983	2-3rd	1f
11 mi. s. Dixonville,AB	*Heracleum lanatum*	27 July 1983	1-3rd	not emg.
Twin Lks.(n.Manning),AB	*Heracleum lanatum*	25 July 1983	4-5th, 2-4th	2m
southern Alberta & Saskatchewan				
Coleman area, AB	*Angelica dawsoni*	27 July 1981	3-e, 2-1st, 3-2nd	no emg.
Coleman area, AB	*Angelica dawsoni*	18 August 1981	1-1st, 2-3rd, 1-5th	no emg.
Coleman area, AB	*Angelica arguta*	18 August 1981	1-2nd, 7-3rd, 6-4th, 8-5th	no emg.
9 mi se Beaver Mines,AB	*Angelica arguta*	19 August 1981	1-4th	no emg.
9 mi se Beaver Mines,AB	*Angelica dawsoni*	21 August 1982	1-3rd	no emg.
9 mi se Beaver Mines,AB	*Heracleum lanatum*	21 August 1982	1-5th	no emg.
Waterton Park, AB	*Angelica arguta*	27 July 1981	35 larvae, 1st & 2nd instar	no emg.
Waterton Park, AB	*Angelica arguta*	19 August 1981	c.100 larvae, mostly 5th	6m, 8f
Waterton Park, AB	*Angelica dawsoni*	19 August 1981	1-5th	1m
Waterton Park, AB	*Lomatium dissectum*	19 August 1981	6+ larvae, 4th & 5th	2m, 3f
Waterton Park, AB	*Heracleum lanatum*	19 August 1981	1-5th	no emg.
Waterton Park, AB	*Angelica arguta*	21 August 1982	5-2nd, 5-3rd, 3-4th, 4-5th	1f
Waterton Park, AB	*Angelica dawsoni*	21 August 1982	1-3rd	no emg.
Waterton Park, AB	*Lomatium triternatum*	21 August 1982	1-4th	no emg.
Waterton Park, AB	*Heracleum lanatum*	21 August 1982	3-5th	2f
Waterton Park, AB	*Angelica arguta*	29 August 1983	1-2nd, 4-4th, 15-5th	3f
Waterton Park, AB	*Heracleum lanatum*	29 August 1983	1-5th	no emg.
Eston, Sask.	"garden dill"	September 1955	larvae prod. both yel. & bl. adults - Hooper (1973:65)	
western US				
Gothic, Colorado	*Angelica ampla*	2-3 Aug. 1980	1-1st, 2-3rd, 16-4th, 18-5th	1f

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. machaon X *zelicaon* - Hybrid zone, Umbellifers				
northern region				
Faust, AB	*Heracleum lanatum*	5 July 1984	3-2nd, 3-3rd	2m
22 km e Slave Lake	*Heracleum lanatum*	5 July 1984	5-1st, 2-2nd, 2-3rd	1m, 1f
Fox Creek, AB	*Heracleum lanatum*	10 July 1982	1-1st, 3-2nd, 9-3rd, 7-4th	not reared
Fox Creek, AB	*Heracleum lanatum*	14 August 1982	2-4th, 2-5th	1f
Fox Creek, AB	*Angelica genuflexa*	14 August 1982	1-5th	not emg.
30 km e Fox Creek, AB	*Heracleum lanatum*	13 July 1984	3-1st, 6-2nd, 1-4th	no emg.
7 mi. s. Whitecourt, AB	*Heracleum lanatum*	10 July 1982	1-5th	no emg.
Cherhill, AB	*Heracleum lanatum*	10 July 1982	1-5th	no emg.
Ft. Saskatchewan, AB	garden celery	9 August 1984	1-5th	1m
Rock Lake, AB	*Heracleum lanatum*	29 August 1982	4-5th (A. Nimmo, leg.)	1f
3 mi n Moberly Lkt., AB	*Heracleum lanatum*	13 July 1982	2-1st, 3-2nd	no emg.
Switzer Park, AB	*Zizia aptera*	5 July 1980	2-e, 2-2nd, 1-3rd, 1-4th	2m
Switzer Park, AB	*Zizia aptera*	17 July 1981	2-e, 1-2nd	not emg.
Switzer Park, AB	*Zizia aptera*	13 July 1982	1-2nd	not emg.
Switzer Park, AB	*Heracleum lanatum*	13 July 1982	8-1st, 2-2nd	no emg.
Switzer Park, AB	*Heracleum lanatum*	2 Aug. 1982	38-1st & 2nd,2-3rd,2-4th,1-5th: no emg., Pike -pers. comm.	
central region				
3 mi. sw. Thorsby, AB	*Heracleum lanatum*	15 July 1982	1-5th	included with Buck Lk.
e. of Buck Lk., AB	*Heracleum lanatum*	16 July 1982	2-2nd, 5-3rd, 6-4th, 27-5th	5m, 5f
Rimbey, AB	*Heracleum lanatum*	16 July 1982	2-4th	1f
7 mi. w. Sylvan Lk.,AB	*Heracleum lanatum*	16 July 1982	1-3rd	1f
19 mi. e. Nordegg, AB	*Heracleum lanatum*	17 July 1982	11-1st, 10-2nd, 1-3rd	4m
2 mi. s. Nordegg, AB	*Heracleum lanatum*	17 July 1982	1-1st	no emg.
4 mi e Elm Cr. Cpgd.,AB	*Zizia aptera*	17 July 1982	1-2nd	
10 mi e Limestone Mt,AB	*Heracleum lanatum*	17 July 1982	1-3rd	no emg.
Didsbury, AB	"parsnip"	? ? 1908	produced 1 m (form *nitra*), in Canadian National Collection	
Waiparous Cpgd., AB	*Zizia aptera*	20 July 1981	4-2nd	no emg.
southern region				
3 mi se. Bragg Creek,AB	*Zizia aptera*	12 & 14 July 80	8 larvae, 1st & 2nd	no emg.
3 mi se. Bragg Creek,AB	*Zizia aptera*	18 July 1982	1-3rd	no emg.
3 mi se. Bragg Creek,AB	*Zizia aptera*	18July- 7Aug.82	11-1st, 20-2nd, 6-3rd, 4-4th	11m, 13f
Chain Lks. Prov. Pk.,AB	?*Angelica arguta*	18 July 1982	2-3rd E.M. Pike - pers. comm.	not reared

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Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained	
P. polyxenes X *machaon* - Hybrid Zone					
Somme, SK	"parsnip"	Sept. 1977	? instars	D. Hooper leg. & colln.	1m
Weekes, SK	"parsnip"	Sept. 1977	? instars	D. Hooper leg., SMNH colln.	1m, 2f
Fort Qu'Appelle, SK	"carrot"	c. 1977	one larva	R. Hooper leg.(pers. comm.)	not emg.
Gypsumville, MB	*Zizia aptera*	1982	? instar	P. Klassen leg. & colln.	1m
Duck Mt. Prov. Park,MB	*Zizia aptera*	23 June 1980	1-2nd, 1-3rd	FAHS leg. & colln.	1f
Duck Mt. Prov. Park,MB	*Zizia aptera*	reared 1982	? instars	J. Troubridge leg.	3m,5f in FAHS colln.
Riding Mt. Nat. Pk.,MB	*Zizia aptera* - foodplant determined in Heron & Robinson (1976)	18-25 June 1955	"several hundred eggs and newly hatched larvae"		-Remington (1956)
Riding Mt. Nat. Pk.,MB	"wild parsnip" & "meadow parsnip"	2 July 1978	? instars	P. Klassen leg. & colln.	2m,1f
Riding Mt. Nat. Pk.,MB	*Zizia aptera*	21-22 June 1980	11-2nd & 3rds, 1-4th		no emg.
Rid. Mt. Park area, MB	*Zizia aptera*	1982	?inst. (prod. 40 pupae)	H. Kimmich leg. & colln.	?emg.
Rid. Mt. Park area, MB	*Zizia aptera*	19 July 1977	? instars	J. Troubridge leg. & colln.	?emg.
Clan William, MB	"parsnip"	Sept. 1970	? instars	R. Hooper colln.	1m,1f
Gladstone, MB	*Zizia aptera*	20 June 1983	4-1st & 2nds	P. Klassen leg.,FAHS colln.	1m,1f
Culross, MB	"parsley"	23 July 1977	"mature larva"	P. Klassen leg. & colln.	1m
Culross, MB	*Zizia aptera*	30 June 1982	? instar	P. Klassen leg. & colln.	1f

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